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BIOLOGICAL INVESTIGATIONS OF LAKE WINGRA

Paul C. Baumann, et al

Wisconsin University

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Interpretations of data ~~collected during this study~~ reveal several important considerations for models of lake systems and future studies of Lake Wingra. Phytoplankton associations, for example, appear to be adaptive, self-organizing systems. Such behavior suggests the possibility to apply optimization principles to phytoplankton models. The data suggest, furthermore, that optimization analysis can be based on size particle distributions of the phytoplankton, which, rather than species, appears to be the basis of phytoplankton categories. Zooplankton and benthos analyses, on the other hand, indicate that energy and nutrient fluxes may be adequately approximated by simulating only a few species. Finally, results of fish studies imply that models of whole lake ecosystems must account for the mobility of predators in estimating their impact on prey populations, which should be characterized by differing spatial and temporal susceptibility to predation. (CPA)

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BIOLOGICAL INVESTIGATIONS OF LAKE WINGRA

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ABSTRACT

An investigation of seasonal changes in species diversity and biomass of phytoplankton, zooplankton, benthos, and fish in Lake Wingra, Madison, Wisconsin, was conducted during 1970 and 1971. The objective of this study was to obtain ecological data on the biological components of an aquatic ecosystem and to utilize these data along with concurrent chemical data to aid the development of systems models of nutrient and energy fluxes in lake drainage basins.

Interpretations of data gathered during this study reveal several important considerations for models of lake systems and future studies of Lake Wingra. Phytoplankton associations, for example, appear to be adaptive, self-organizing systems. Such behavior suggests the possibility to apply optimization principles to phytoplankton models. The data suggest, furthermore, that optimization analysis can be based on size particle distributions of the phytoplankton, which, rather than species, appears to be the basis of phytoplankton categories. Zooplankton and benthos analyses, on the other hand, indicate that energy and nutrient fluxes may be adequately approximated by simulating only a few species. Finally, results of fish studies imply that models of whole lake ecosystems must account for the mobility of predators in estimating their impact on prey populations, which should be characterized by differing spatial and temporal susceptibility to predation.

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SECTION I

CONCLUSIONS

Data from this project are useful to development of lake ecosystem models. Principal finds are:

1. Seasonal succession of phytoplankton is an example of an optimization process. The assemblage may, therefore, be treated as one category or perhaps several categories of different sized particles without information loss.

2. Low nutrient levels coupled with high phytoplankton production rates indicate that nutrient recycling is the chief source of nutrients sustaining production.

3. Only a few macrozooplankton dominate transfer and transformation of energy and nutrients at the primary consumer trophic level.

4. Microzooplankton, predominantly rotifers, are not major components in energy and nutrient cycling and may, therefore, be neglected entirely.

5. Benthos is dominated by one species that may also be the chief open water food source for fish.

6. Fish diurnal movements must be considered in any attempt to describe their effect on prey populations.

7. Some attempt should be made to allow for spatial and temporal segregation of predator and prey organisms for models to capture the dynamic qualities of whole lake ecosystems.

SECTION II

RECOMMENDATIONS

Three recommendations concerning the scope of whole lake system models can be made:

1. Lake systems tend to be tightly structured communities. Nutrient recycling must, therefore, be an integral part of any model.

2. Temporal and spatial variations of the biota will present problems to simulation models. The only boundaries really applicable to the lake are limits of the water system. Habitat variability within the lake must, therefore, be accounted for in models.

3. Species may be aggregated into larger functional categories and may be categorized either as a group (e.g. nannoplankton) or by studies of representative species (e.g. bluegill sunfish for pan fish).

Future work could concentrate on some interesting problems. Because Lake Wingra is only a single lake, the generality of the conclusions reached here should be tested against other lakes. Furthermore, the data suggest that temperature and light are the most significant variables in the system. Such a situation indicates that energy constraints may play a decisive role in the structure of the lake ecosystem. Such a possibility deserves more consideration. Finally, the tightly linked trophic structure of the lake suggests some interesting experimental manipulations to determine causal relationships in the development of various noxious conditions associated with eutrophication.

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SECTION III

INTRODUCTION

Ecological data on biological components of aquatic ecosystems are vital to the development and implementation of systems models of nutrient and energy flows in lake drainage basins. Such data serve to identify key nutrient pathways and guide the formulation of realistic process submodels. Two separate but interrelated systems modeling programs have selected Lake Wingra as a study area. One, also funded by this EPA grant, (Huff et al.) is concerned with nitrogen and phosphorus movement through the Lake Wingra Basin. The other is the US/IBP Eastern Deciduous Forest Biome Project, which is studying and modeling physical, biological and chemical processes in the Lake Wingra Drainage Basin. Both of these modeling efforts rely on ecological baseline data and insight into the processes controlling energy and nutrient flow through ecosystems. Upon this foundation of interacting data gathering and modeling, refinements in systems models may evolve and not only enhance understanding of ecosystem functioning, but also provide insight into the most sensitive parameters in the system. As a tool in modeling the Lake Wingra drainage basin, therefore, the present project deals with characterization of seasonal changes in species-diversity and biomass of phytoplankton, zooplankton, benthos, and fishes in Lake Wingra.

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SECTION IV

OBSERVATIONS OF NATURAL PHYTOPLANKTON ASSOCIATIONS

Introduction

An interesting aspect of phytoplankton ecology is seasonal change in the pattern of species composition. This periodicity of phytoplankton populations has been observed in every aquatic ecosystem studied and has been documented thoroughly in many studies (e.g., International Association of Limnology, 1971). Despite years of research effort, however, the explanation of the complex interrelationships existing within a phytoplankton community remains an unfulfilled goal. To be sure, physiological mechanisms and population dynamics have been related to environmental and biological factors in aquatic ecosystems. Literature reviews (e.g., Hutchinson, 1967), for example, reveal correlations of temperature, light, nutrient concentration, zooplankton grazing, and parasitism with the appearance and disappearance of both individual and groups of phytoplankton species.

Changing patterns of species composition indicate that phytoplankton associations are dynamic systems (cf. Lund, 1964). Individual species may vary in their tolerance to environmental fluctuations, but the overall diversity and composition of the association ultimately reflect all of the selective pressures in their ecosystem. Sager (1967) has discussed the importance of measures of phytoplankton diversity as an indicator of the "condition" of a lake ecosystem. Such measures when compared among lakes emphasize response differences of phytoplankton associations. Within a single lake, multivariate analysis techniques (e.g., Allen and Koonce, in prep.) indicate that changing species composition pattern actually reflects varying dominance strategies. Such analyses, for example, identify major algal stratagems (i.e., slow growth rate, but wide tolerance to environmental fluctuations or rapid growth rate, but restriction to well-defined regimes of light and temperature) and indicate when these various stratagems result in species predominance. Of themselves, however, observations of the dynamic nature of environmental fluctuations and the correlated response of species in an association shed little light on the exact mechanisms operating, but form a foundation from which to evaluate the important principles involved.

In order to study the underlying principles governing the mechanisms which cause phytoplankton periodicity, an investigation of the phytoplankton in Lake Wingra was initiated.

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Study Site

Lake Wingra (Fig. 1) is a small shallow lake within the City of Madison, Wisconsin. The lake has a surface area of 136 hectares, a maximum natural depth of 4.2 meters, and an average open water depth of 2.5 to 3.0 meters. The lake is primarily spring fed, but five storm sewers provide intermittent water supply to the lake. Much of the southern shore of the lake belongs to the University of Wisconsin Arboretum and is an undisturbed forest. The northern shore is dominated by recreational and residential areas.

Methods

At weekly intervals from 3 March 1970 until 23 February 1971 and periodically thereafter until mid-April 1971, water samples were collected at one station (Fig. 1) for estimation of primary production, phytoplankton identification and enumeration, and chemical analyses. Water samples were collected with a 2-liter nonmetallic Van Dorn sampler at three depths (0, 1, and 2 meters) in the water column.

Estimation of primary production were based on standard *in situ* four hour incubations of duplicate light and dark bottles containing 125 ml of sample water to which 2 µci of $NaH^{14}CO_3$ were added. Sample bottles were suspended horizontally on specially constructed racks from a clear plexiglas float. During collection and inoculation, samples were protected from light shock by conducting both procedures under a canvas tarp. After the four hour incubation period, phytoplankton samples were fixed with 0.5 ml of Lugol's solution, returned to the laboratory and filtered through 0.47 µ, membrane filters under a vacuum of 0.17 atm. The filters were dried for at least two hours in a dessicator over silica gel, exposed to concentrated HCl fumes for ten minutes, and redried in a dessicator for at least 30 minutes. Radioactivity of the filters was then measured with a thin window, gas flow, planchet counter in the Geiger-Müller range. ^{12}C fixation was calculated from the following formula:

$$^{12}C_{fixed} = {}^{12}C_{available} \cdot \frac{^{14}C_{fixed}}{^{14}C_{available}} \cdot k_1 \cdot k_2 \cdot k_3$$

where k_1 = counter efficiency

k_2 = isotope discrimination factor

k_3 = bottle factor

Integral production over depth was determined planimetrically, and the day rate was calculated from: $P_T = P_I \cdot R_T/R_I$

where P_T is total production/m^2/day, P_I is measured production/4 hr, R_T

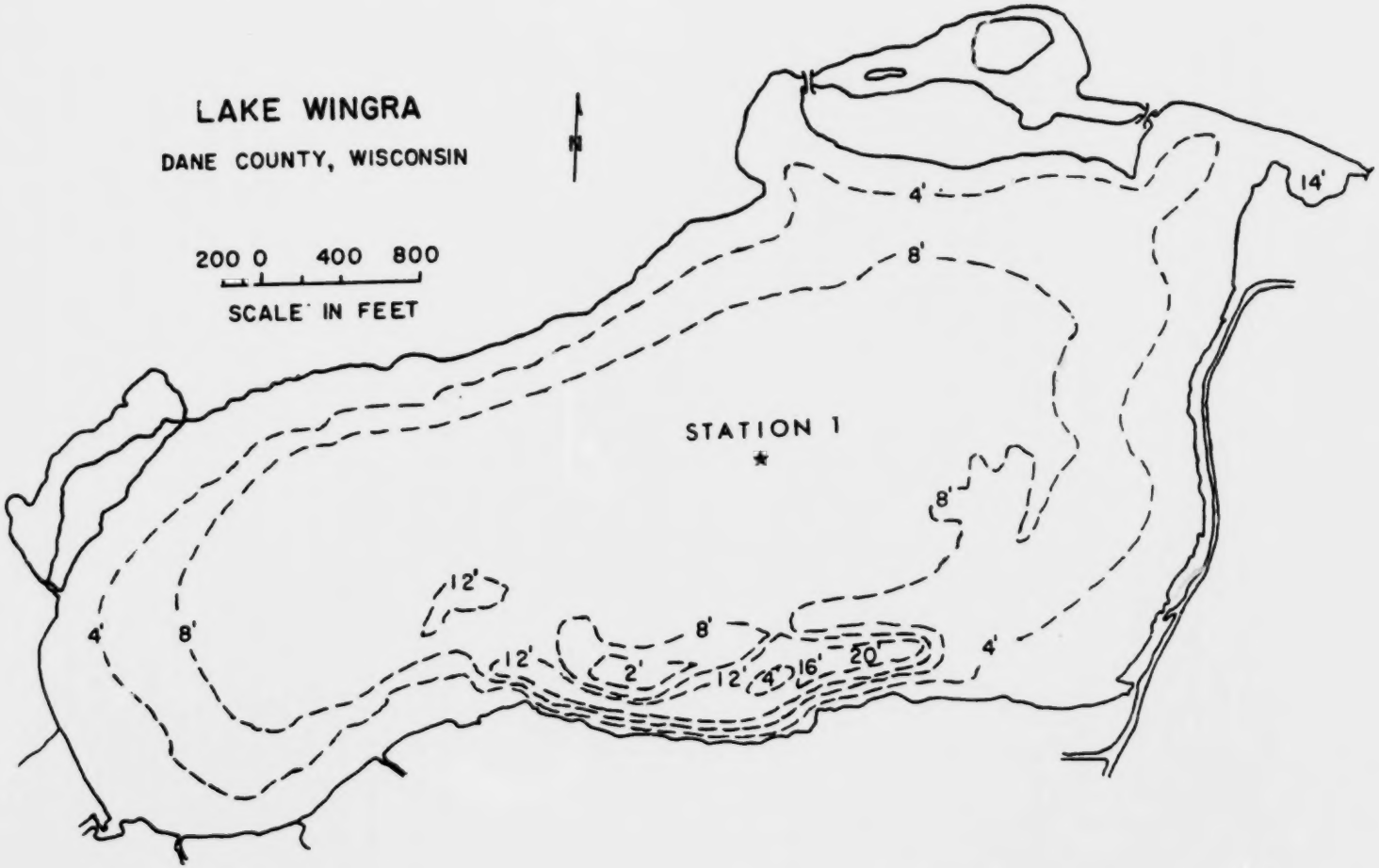

Figure 1. Hydrographic map of Lake Wingra. (To convert scale in feet to meters, multiply by 0.305.)

is total incident radiation, and R_I is the incident radiation during the incubation period. Such a direct proportion seemed reasonable in Lake Wingra from 2 hour incubations conducted over an entire day. Incident solar radiation data were obtained from the U. S. Weather Bureau at Truax Field, Madison, Wisconsin.

Following the start of the ^{14}C incubation period, approximately three liters of water were collected from each sampling depth and returned to the laboratory for chemical analysis. Water analysis was conducted by routine procedures outlined in Table 1. Conductivity, pH, alkalinity, and free CO_2 were measured shortly after return from the field. Nitrate and ammonia analyses were run on the same day samples were collected, but phosphorus, iron, and silica, although prepared for analysis, were not run until the following day. Samples for iron and phosphorus analyses were transported in 300-ml glass bottles and all other samples in 1-liter polyethylene bottles. Prior to sampling, all sample collection bottles were acid washed with 1:1 HCl and rinsed repeatedly with tap then distilled water. As a final precaution, all sample bottles were rinsed with sample water before filling.

After water sample collection, light and temperature profiles were taken. Temperature was measured with a Whitney Underwater Thermistor Thermometer that was calibrated biweekly. White light intensity was measured with a G-M Underwater Light Meter at half meter intervals to the bottom of the lake. The extinction coefficient for white light was calculated from a linear reg ession of the natural logarithm of relative light intensity versus depth:

$$\ln \frac{I_z}{I_o} = -\varepsilon z$$

where ε is the extinction coefficient, z the depth, and I_z and I_o the light intensity at depth z and the surface, respectively.

Biomass estimates are based on species identification and enumeration of sedimented samples (Utermöhl, 1958). Separate 125-ml aliquots of the incubation samples were fixed with Lugol's solution and preserved for analysis. Depending on the biomass present, either 10 or 25 ml duplicate subsamples of each aliquot were allowed to settle for 12 hours in specially constructed sedimentation chambers. The chambers were then placed on a mechanical stage of an inverted phase contrast compound microscope, and phytoplankton species were identified and counted at 625x. Enough transects (10mm x 0.13mm) were processed to encounter at least 100 individuals of the major species and at least 15 of the minor or rare species. Cell counts were converted to biomass from cell volume calculations (e.g., Pechlaner, 1967). The cell volume of each species was determined by approximating the shape of the species with a solid geometrical formula. In making the conversion from cell volume to biomass, a density of 1 g/ml was assumed for all species.

TABLE 1

SUMMARY OF CHEMICAL ANALYSIS METHODS

Analysis	Method	Sensitivity	Reference
NH_3-N	Distillation	0.02 mg/l	1
NO_3-N	Cadmium Reduction	0.7 µg/l	2
NO_3-N	Brucine	0.1 mg/l	1
PO_4-P	Phospho-molybdate Complexation	1.0 µg/l	3
SiO_3-Si	Silico-molybdate Complexation	3.0 µg/l	2
Iron	Penanthroline	20.0 µg/l	1
Alkalinity	Acid Titration	10.0 mg/l	1
CO_2	Sodium Carbonate Titration	?	1

References:

1. Standard Methods, 1965
2. Strickland and Parsons, 1968
3. Murphy and Riley, 1962

Results

For a great part of the year, there was little or no thermal stratification. As a result, both chemical and biological stratification was limited. The following data, therefore, contain only average or total water column values.

The average temperature of the water column in Lake Wingra varied from 0.5°C to 26.2°C (Fig. 2). The highest temperatures occurred from mid-July to early August. The maximum open water temperature observed was 27.4°C at the surface in late July.

Alkalinity and pH also demonstrated seasonal fluctuations (Fig. 3). Alkalinity ranged from 194 mg$CaCO_3$/liter under ice to 124 mg $CaCO_3$/liter in October. During the same time period, pH values varied inversely with alkalinity from 7.44 to 9.14. The highest pH values occurred in late August and early September. Fluctuations in pH and alkalinity indicate an equivalent fluctuation in total dissolved inorganic carbon from 52 to 28 mg C/liter.

Nitrate concentrations fluctuated from 1 µg N/liter to 610 µg N/liter (Fig. 4). It should be noted that a new analytical procedure was initiated on 1 September 1970 and the sensitivity of the previous nitrate method may not accurately reflect the low nitrate levels prior to that time. Ammonia concentration followed a pattern similar to nitrate (Fig. 4). Both in 1970 and 1971, the highest values were observed a month before ice out. During the ice-free period, however, the concentrations quickly fell below detectable limits (0.02 mg/l).

Concentration of dissolved ortho-phosphorus is low all year (Fig. 5). Only during the winter does the concentration rise to 30 µg P/liter. Much of the year phosphorus concentration is below 10 µg P/liter. Total phosphorus analyses, on the other hand, reveal higher concentrations (Fig. 5), but even at the maximum concentration during July and August, it never exceeded 70 µg P/liter.

Iron and silicate analyses were not run as often as the other analyses, but for the most part, indicate uniformly low levels of iron and seasonally varying silicate concentration (Fig. 6). Silicate concentrations, for example, appear to be greater than 8 mg Si/liter toward the end of the ice-free period, but drop precipitously during the spring diatom bloom. Unfortunately, the iron analytical technique was not sensitive enough for the low levels encountered, but seldom were concentrations in excess of 0.05 mg/liter observed and no seasonal pattern in the data can be detected.

Considering the relatively low levels of nitrogen and phosphorus during the ice-free period, the phytoplankton biomass and productivity in Lake

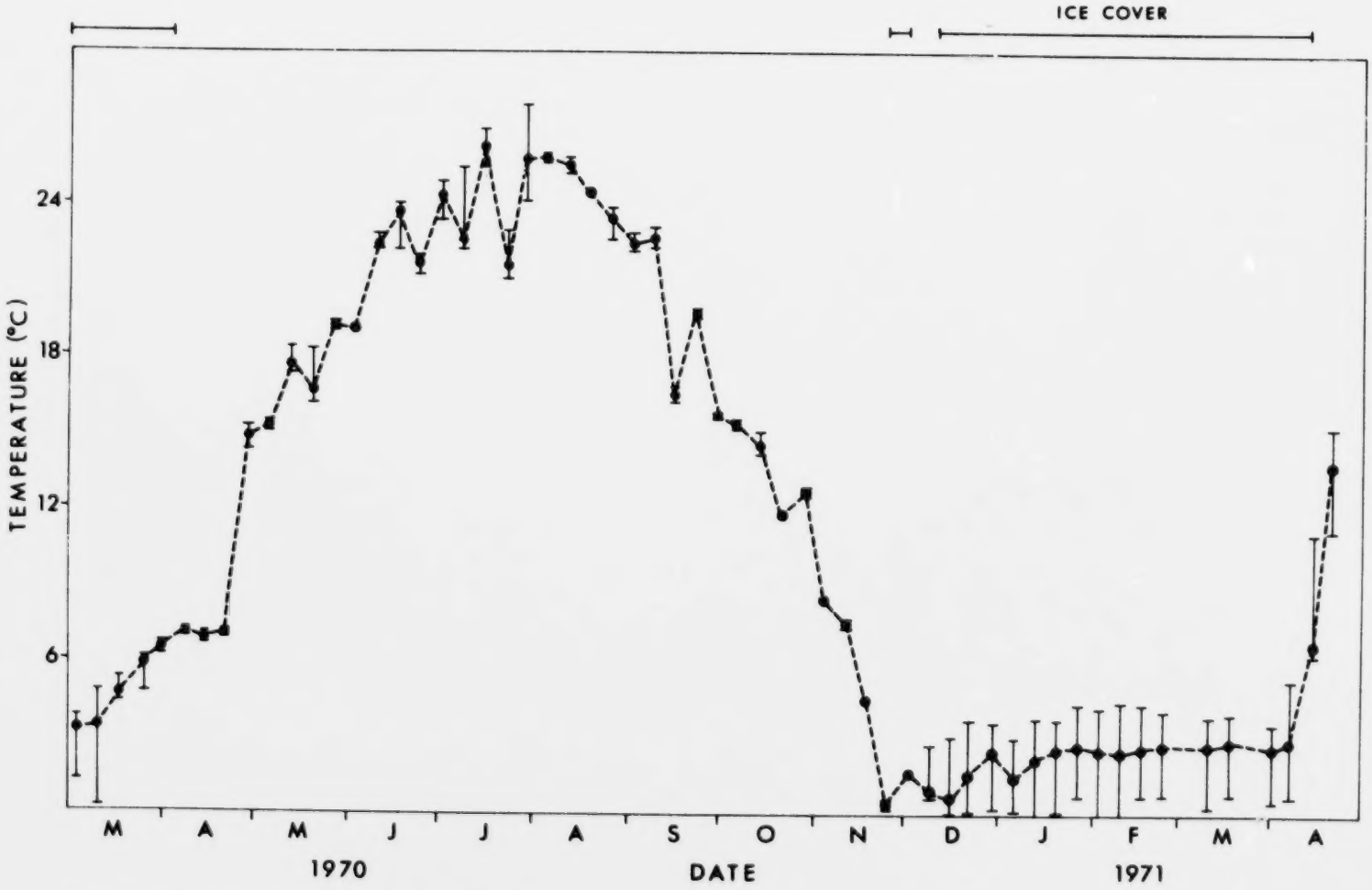

Figure 2. Annual temperature distribution of average water column temperature in Lake Wingra. Bars represent the observed range of temperatures on each measurement day.

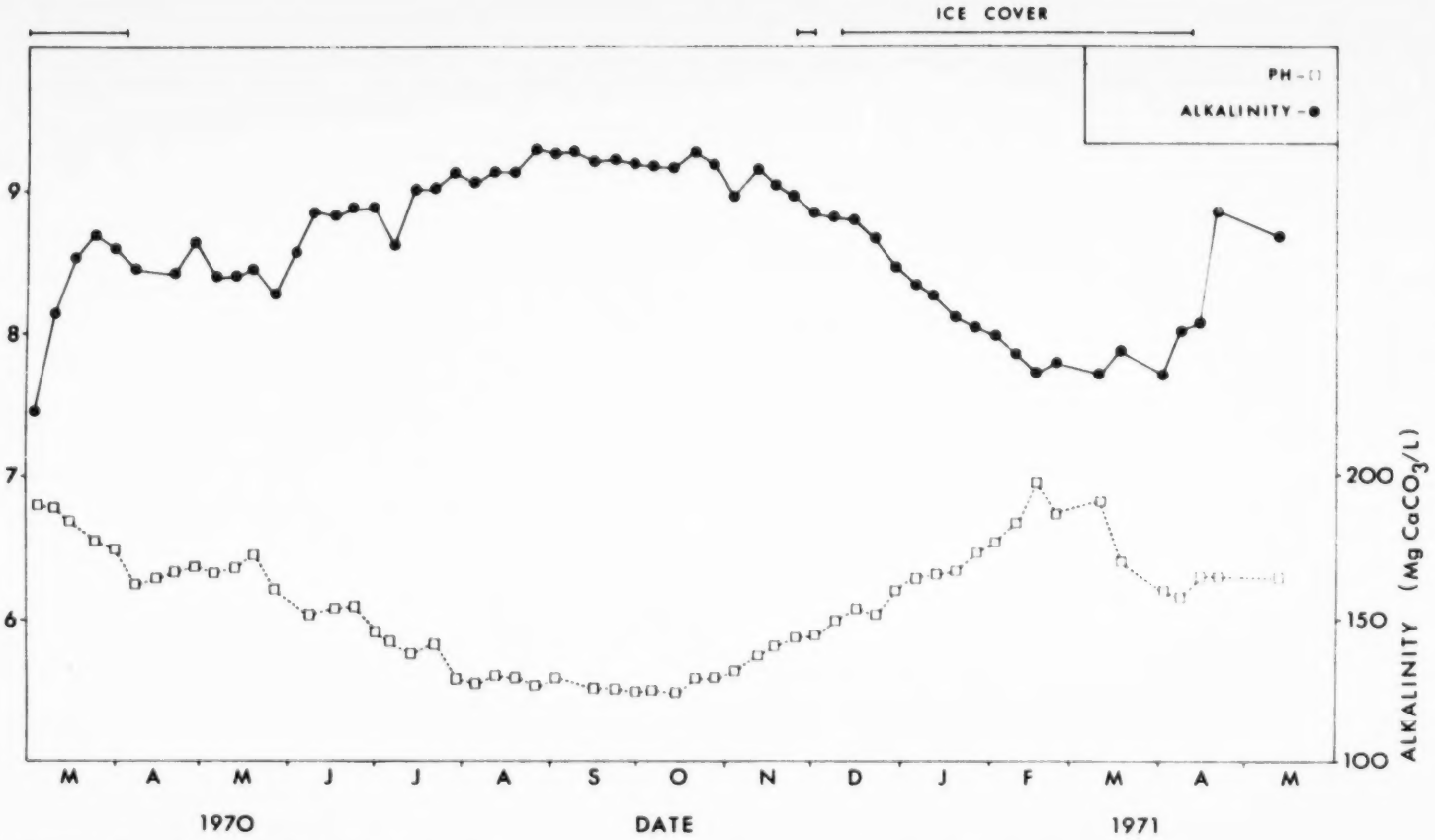

Figure 3. Annual distribution of average water column pH and alkalinity in Lake Wingra.

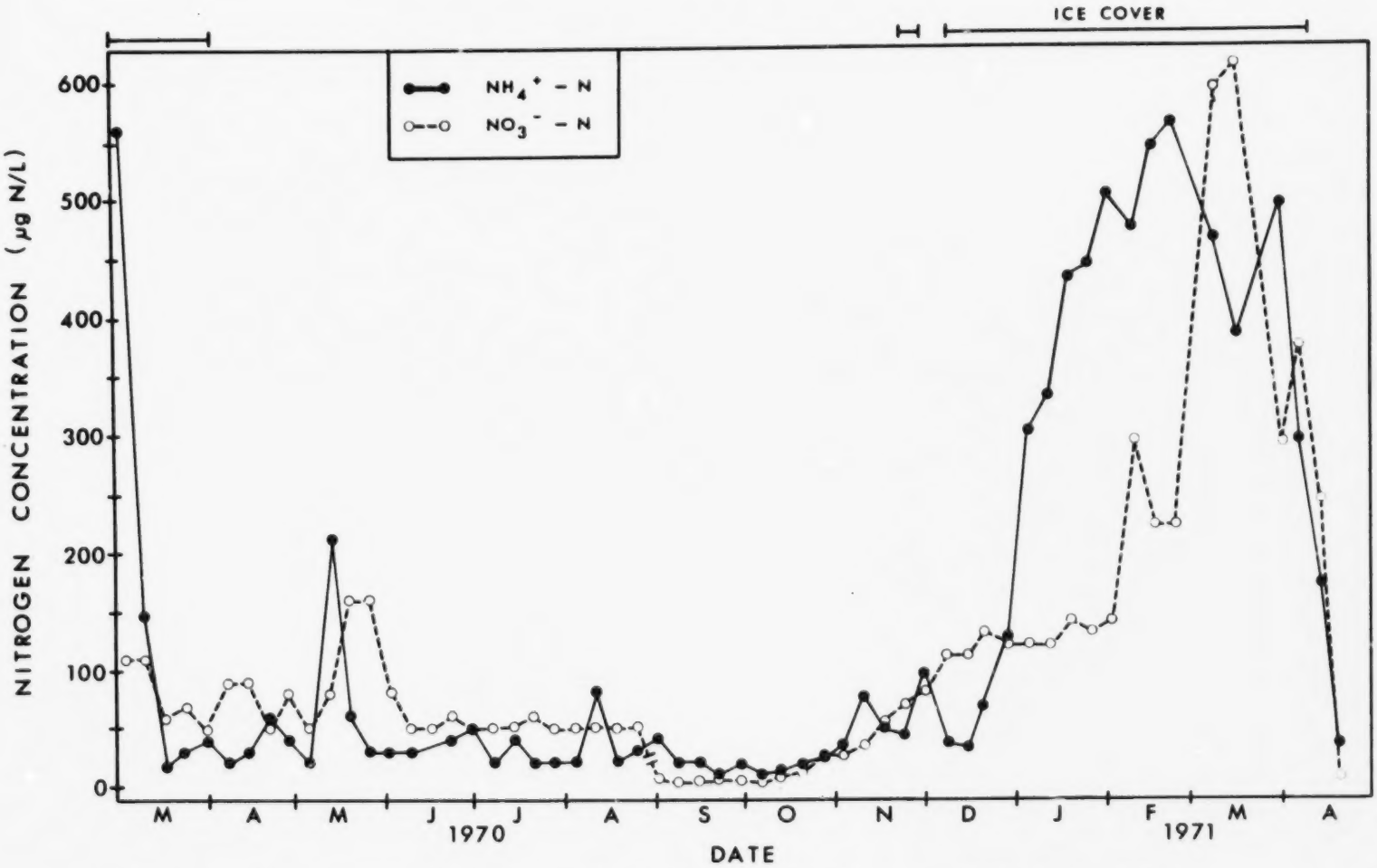

Figure 4. Average ammonium and nitrate concentrations for one year in Lake Wingra.

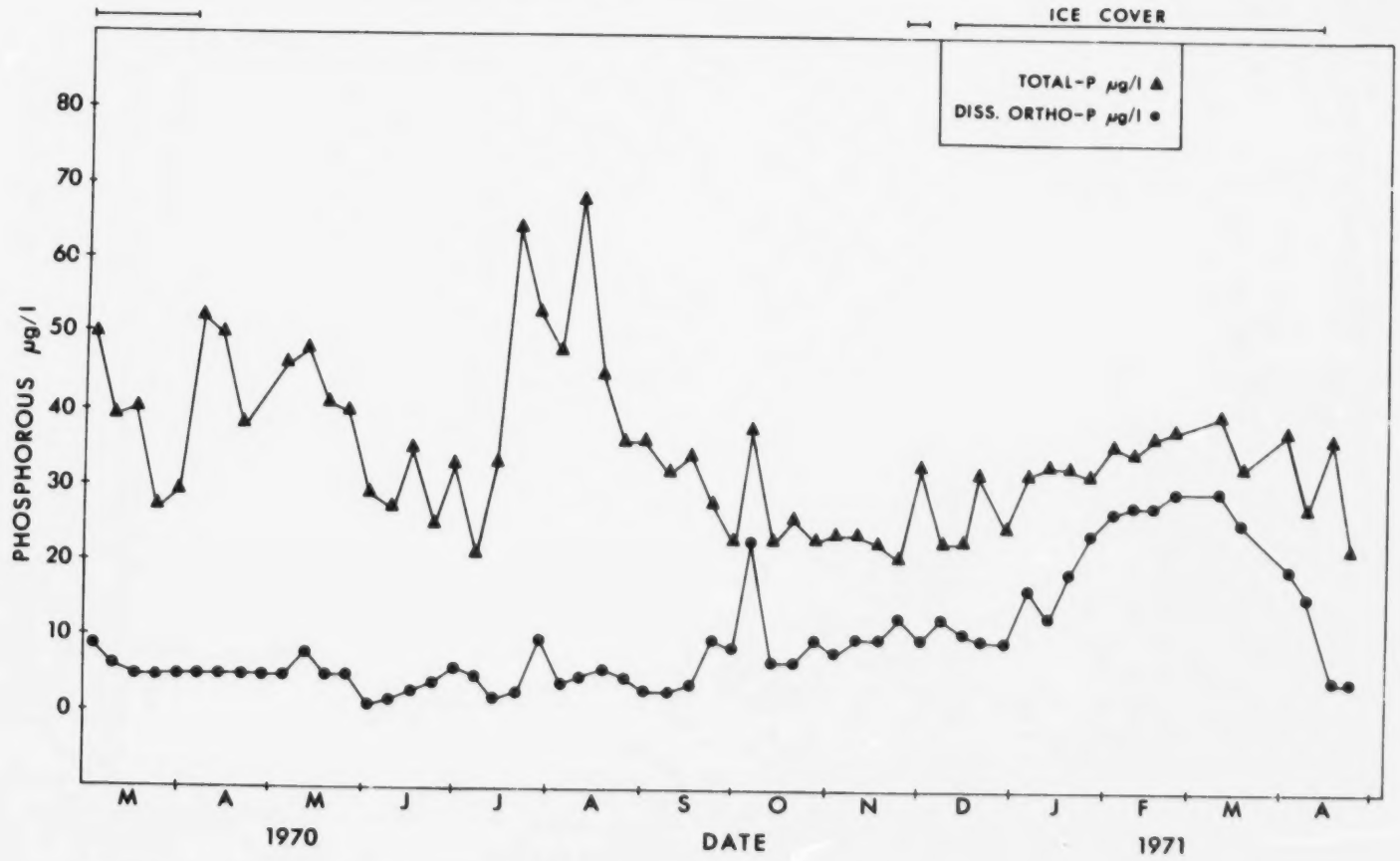

Figure 5. Average total and dissolved ortho-phosphorus concentrations for one year in Lake Wingra.

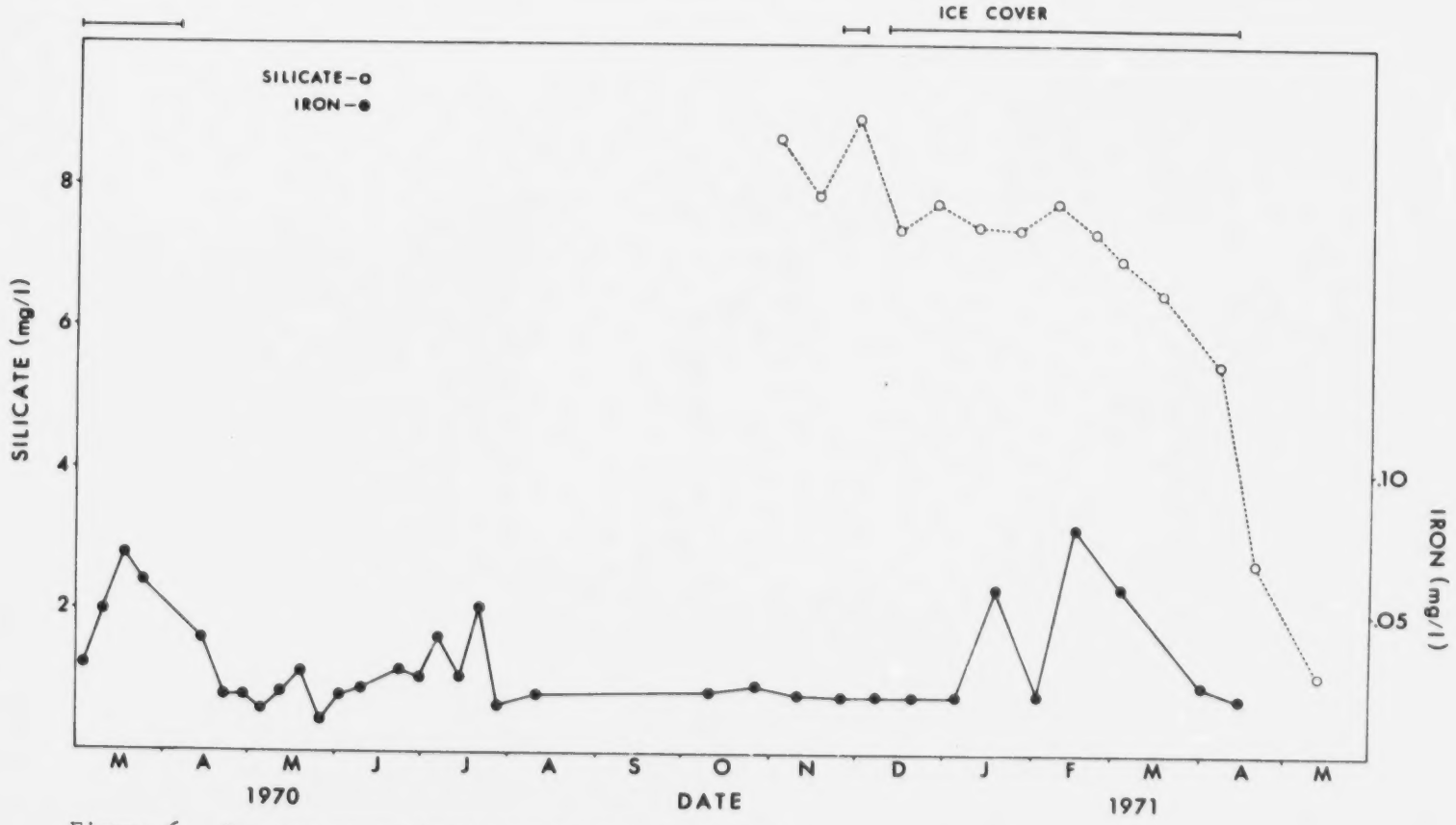

Figure 6. Average concentrations of silicate (as Si) and iron (as Fe) for parts of one year in Lake Wingra.

Wingra are high (Fig. 7). The phytoplankton demonstrates only one pulse in biomass (and that due primarily to one diatom species). The remainder of the ice-free period, biomass is relatively constant (averaging about 20 g freshweight/m^2). Productivity, as measured by ^{14}C uptake, varied from less than 10 mg C/m^2/day to over 7000 mg C/m^2/day, with an annual mean daily productivity of 2400 mg C/m^2/day. These productivity levels are greater than those reported in the literature from any other lake (Wetzel, unpublished summary). Furthermore, productivity in general peaks with maximum light intensity in June and not with temperature in mid-July to August.

An analysis of the taxonomic composition during the course of the study reveals a typical pattern (Fig. 8). Winter associations are dominated by cryptomonads and chrysomonads, spring associations by diatoms, early summer associations are characterized by green coccoid algae and dinoflagellates, midsummer and fall associations are dominated by blue-green algae, and with the beginning of ice cover the association changes to cryptomonads and diatoms. In general, however, the associations at all times of the year are dominated by nannoplankton and ultraplankton (Fig. 9). Flagellated forms are dominant during the ice cover period (Fig. 10), and colonial forms constitute the bulk of the phytoplankton biomass during late summer and fall (Fig. 11).

Discussion

The phytoplankton's temporal pattern and the water chemistry fluctuations reflect to varying degrees the cyclical temperature and light regimes imposed on a temperate lake. In reflecting the cyclical nature of light and temperature, therefore, phytoplankton periodicity in Lake Wingra is similar to a wide variety of other lakes. As indicated in Figure 7, the phytoplankton demonstrates a spring peak in biomass and a poorly defined peak in fall. Although the morphology of Lake Wingra may impose some moderating effect on the "boom-and-bust" cycles observed on other lakes, this basic spring and fall bloom is common to a great many lakes (Pearsall, 1932; McCombie, 1953; Round, 1971).

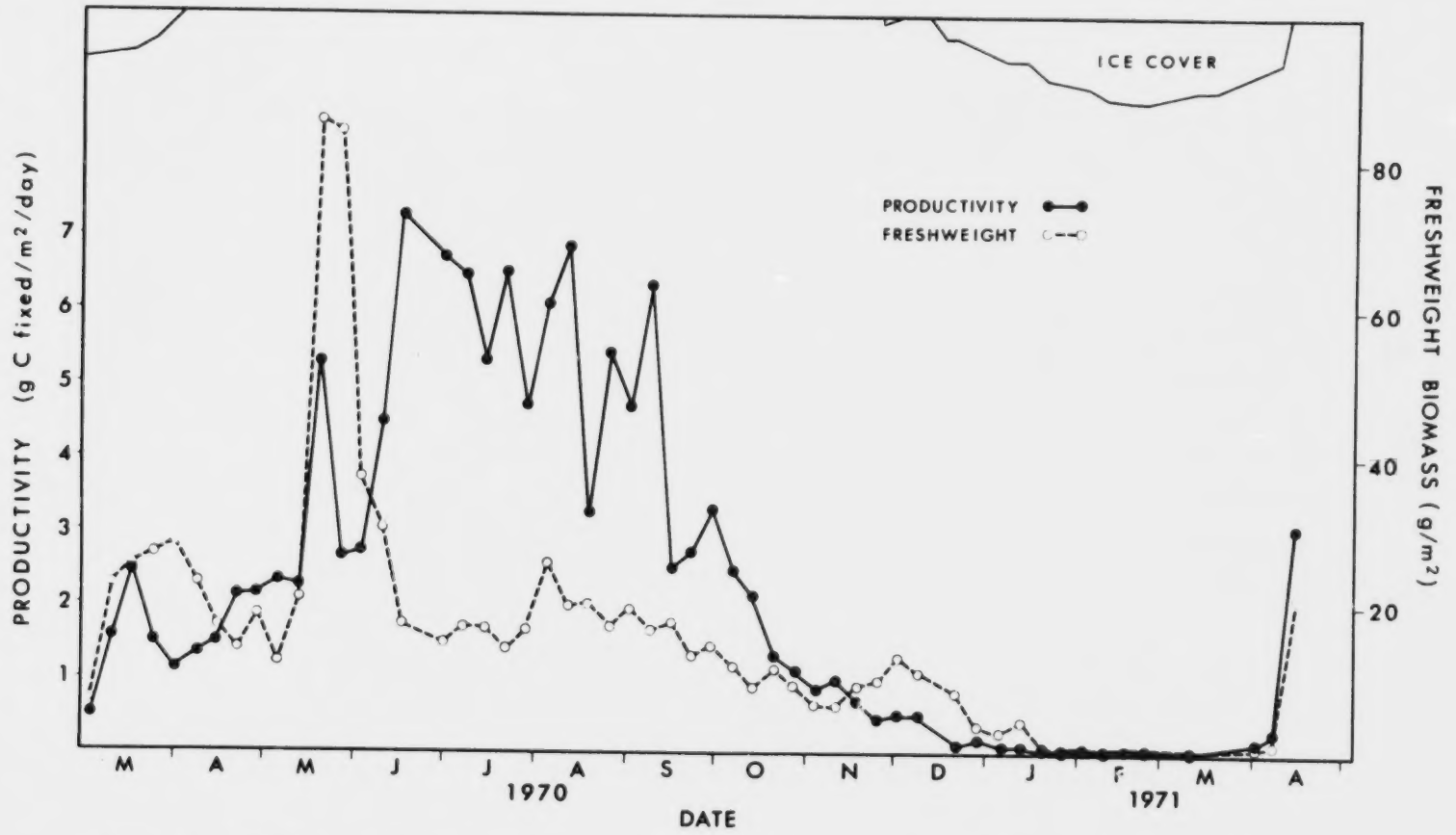

Figure 7. Average daily productivity and freshweight biomass of phytoplankton in Lake Wingra for one year.

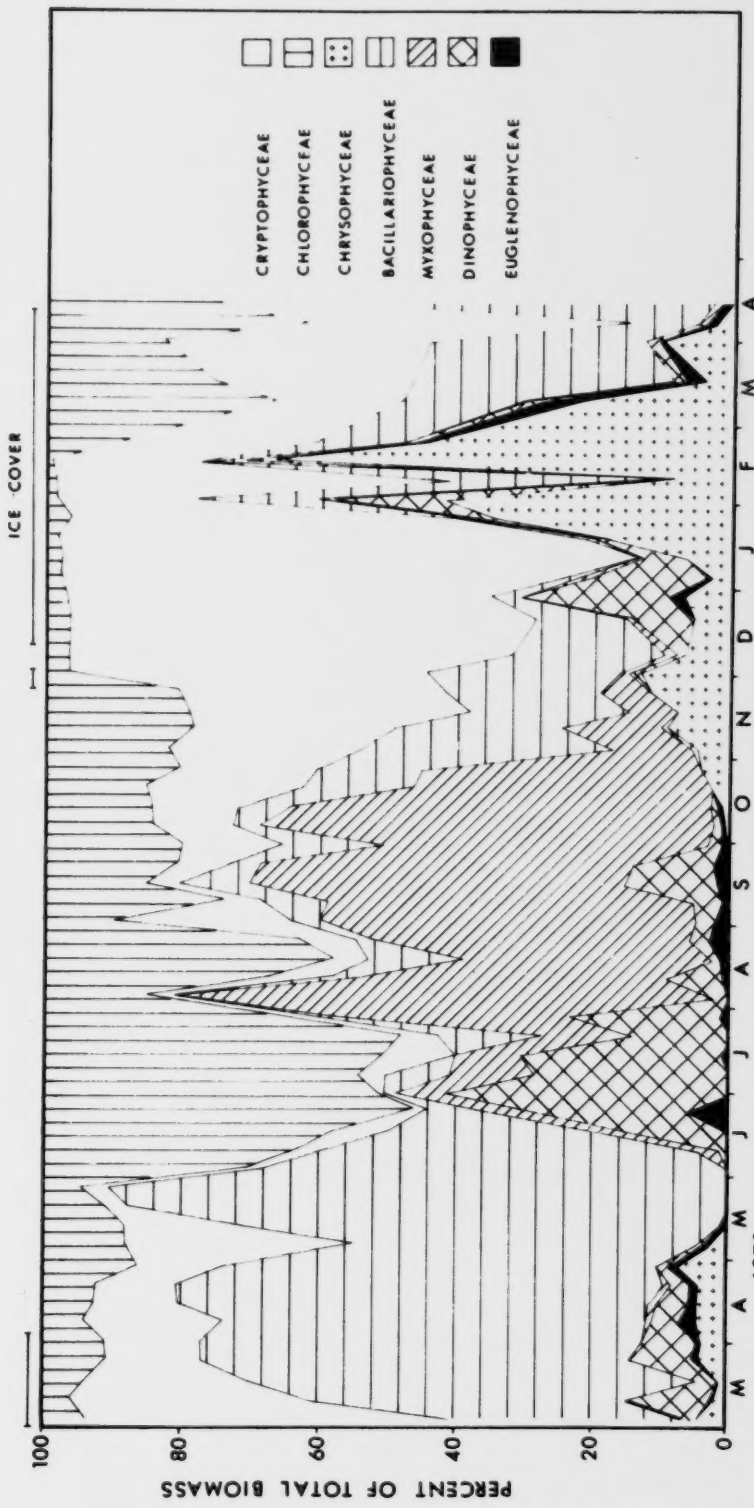

Figure 8. Class composition pattern of phytoplankton in Lake Wingra for one year.

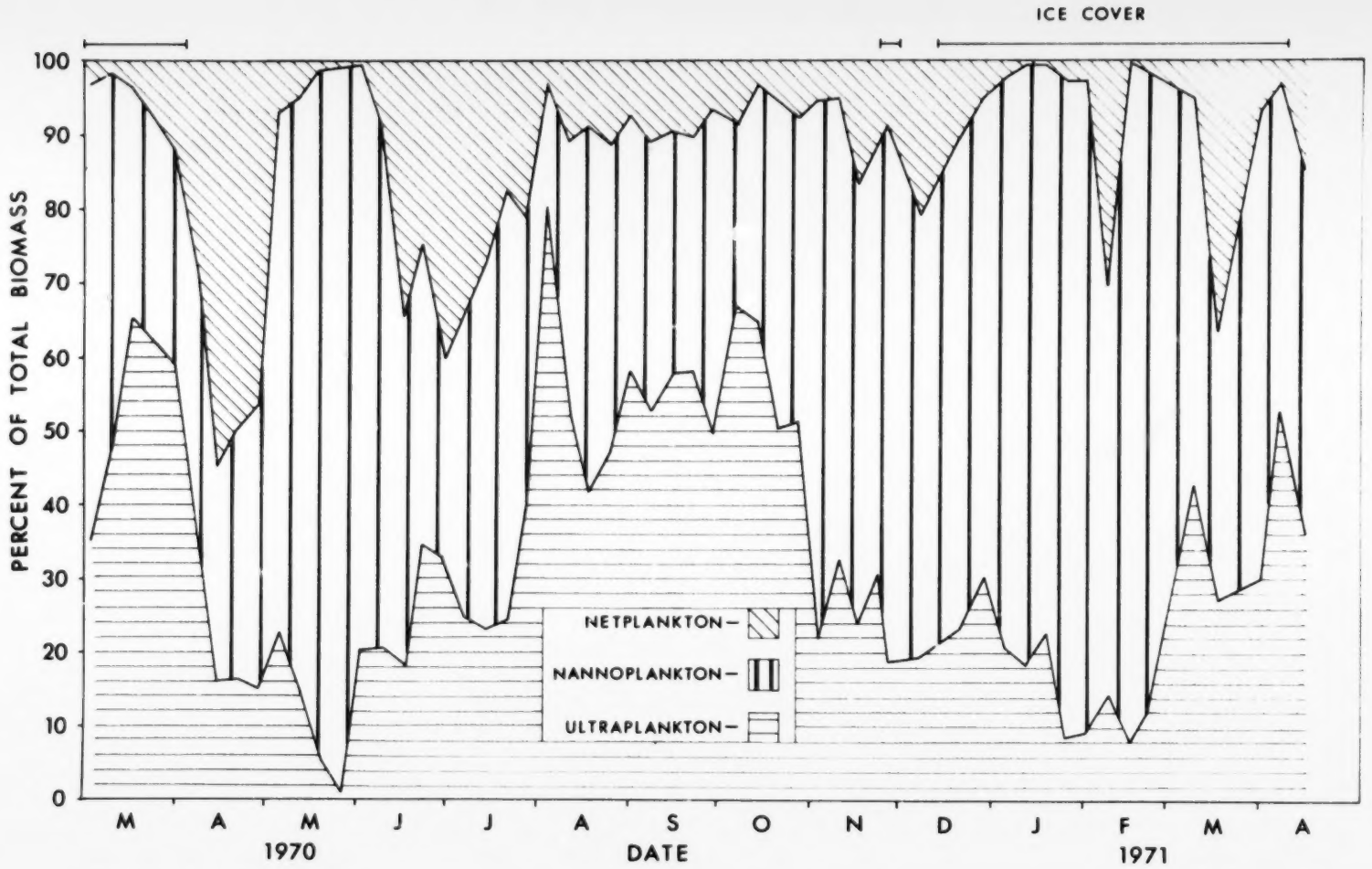

Figure 9. Size distribution of phytoplankton in Lake Wingra for one year. Size categories are netplankton (maximum dimension of cell greater than 50 µm), nannoplankton (maximum dimension of cell less than or equal to 50 µm, but greater than 10 µm), and ultraplankton (maximum cell dimension less than or equal to 10 µm).

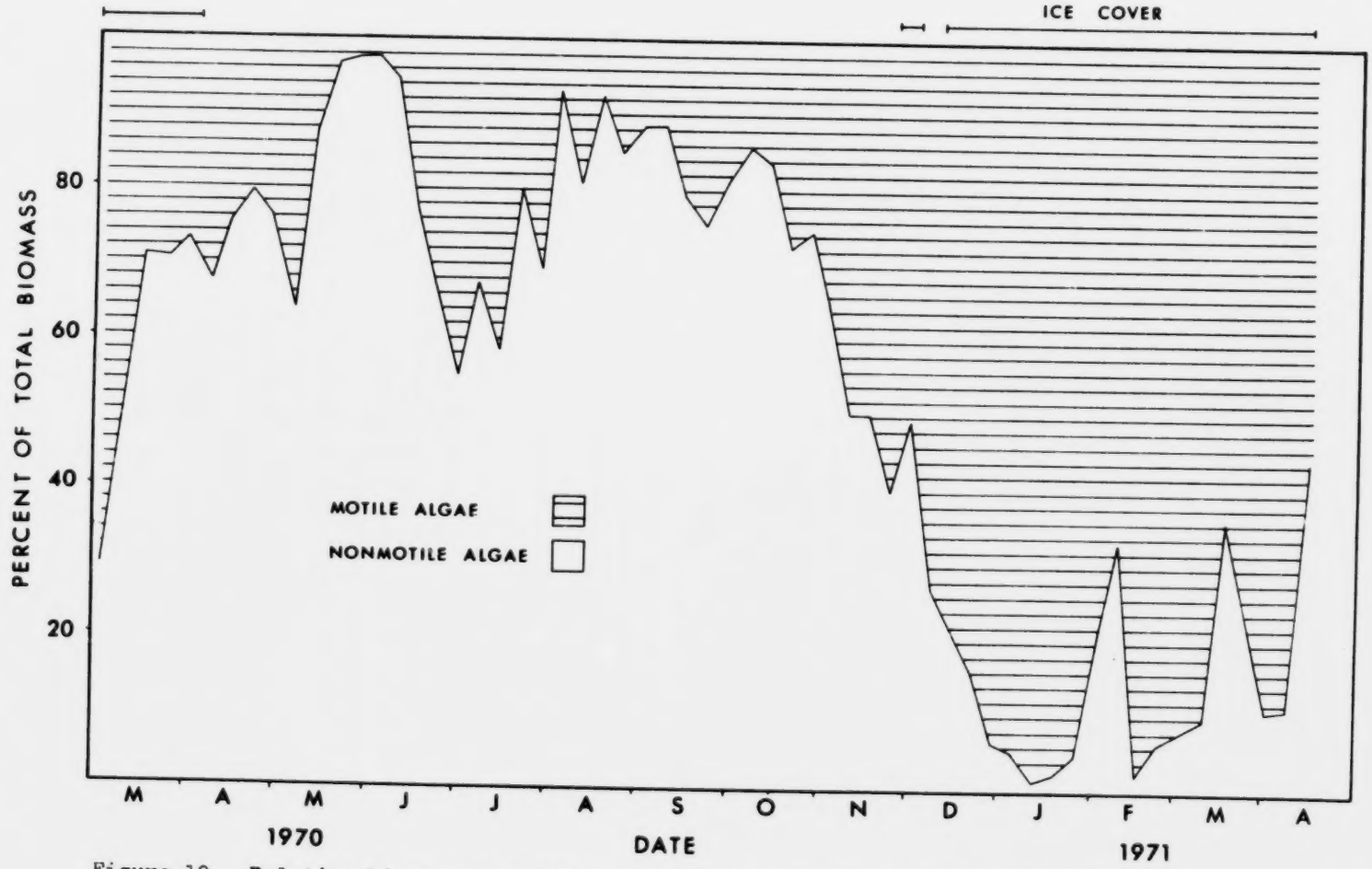

Figure 10. Relative biomass of motile and nonmotile phytoplankton in Lake Wingra for one year.

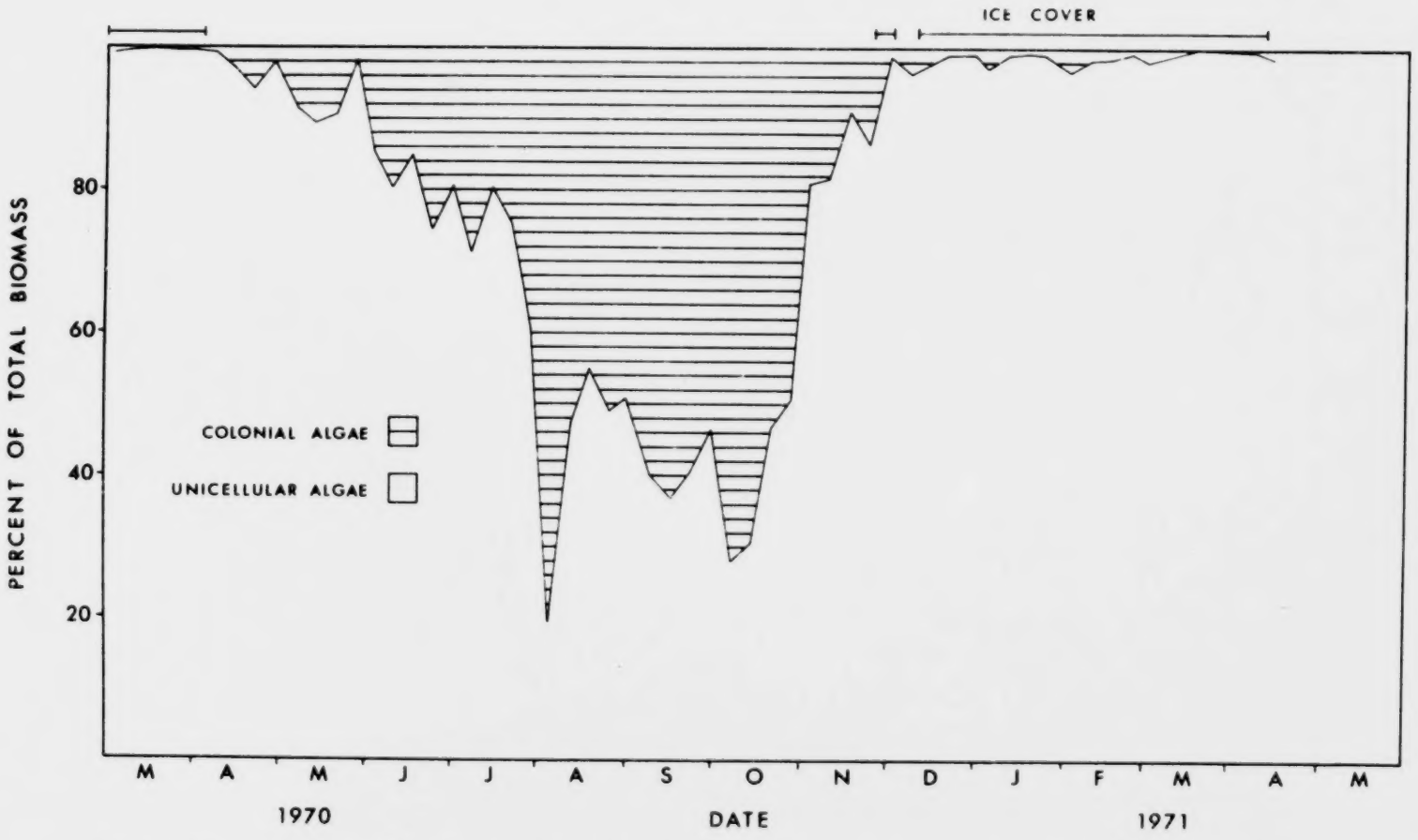

Figure 11. Relative biomass of colonial and unicellular phytoplankton in Lake Wingra for one year.

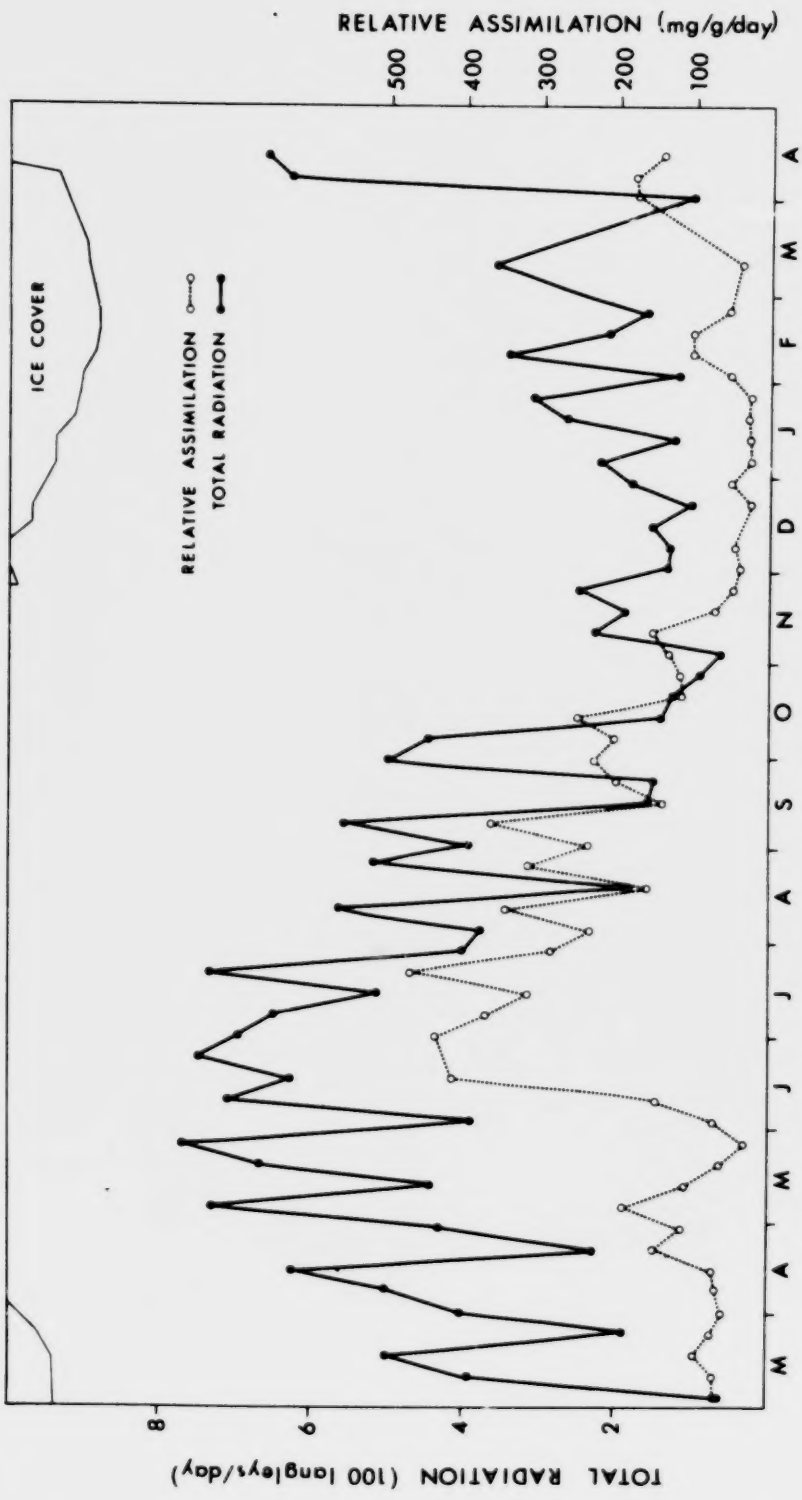

Figure 12. Annual distribution of total incident radiation and relative carbon assimilation rate by phytoplankton in Lake Wingra.

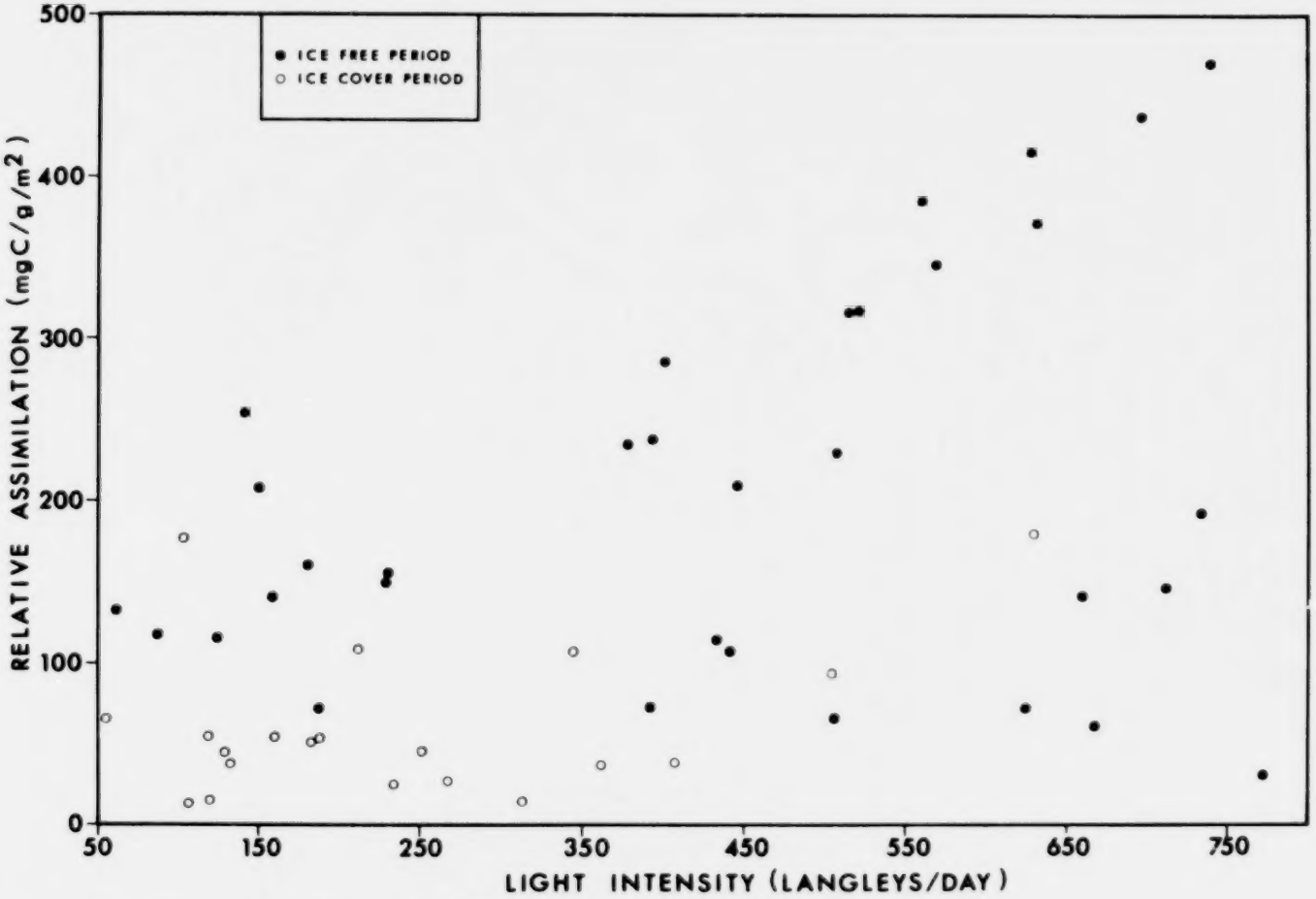

Figure 13. Correlation of total incident radiation and relative carbon assimilation rate by phytoplankton on each observation date for one year in Lake Wingra.

Productivity like standing crop fluctuates seasonally, but its maximum appears to be more associated with longest day lengths and highest temperatures. Again this observation is in accord with those of other investigators (Wetzel, 1966; Goldman and Wetzel, 1963). Of interest, however, is the relationship between incident light and relative assimilation (Figs. 12 and 13). During parts of the year, there appear to be close correlations between light and relative assimilation (Fig. 13), but during other parts of the year, the relationship appears to be obscure at best. The reason for this lack of correlation is not clear. Certainly, other environmental factors are changing during periods of poor correlation, and there are some fairly obvious changes in the composition of the phytoplankton (cf. Fig. 8). Taken as a whole, therefore, the lack of a strong correlation with light may indicate shifting physiological capabilities of the phytoplankton association.

Perhaps the best indication of changing adaptations is the progression of algal Classes during the course of the year. Although the sequence of algal Classes may vary, the succession can be demonstrated in lakes from a wide variety of climatic regimes. In Lake Kinneret (Serruya and Pollingher, 1971), for example, Dinophyceae and Cryptopyceae dominate the plankton from January through June. Subsequently, the Chlorophyceae become more important from July through November. The Myxophyceae do not constitute major fractions of the biomass, but occur primarily in July and August. A somewhat different success pattern has been reproted for Lough Neagh, United Kingdom (Gibson, Wood, Dickson, and Jewson, 1971), but a changing pattern of dominance is still preserved. Alpine lakes, covered by ice for long periods of the year, also reveal changing Class composition patterns with the Myxophyceae assuming far less importance (Pechlaner, 1967 and 1971). The apparent success of algal Classes in the above lakes, and to some extent in Lake Wingra, are due mainly to changes in abundance of a few species. Because of the nature of the species' preadaptations, it is not unreasonable to envisage a changing set of environmental and biological variables selecting out those species or groups of species that will grow most rapidly.

Observations of Lake Wingra phytoplankton indicate some adaptive characteristics of the various algal Classes represented in the lake. Diatoms, for example, appear to grow best during the low temperature periods of spring and fall. Green algae (Chlorophyceae) appear to be best adapted to a 10° to 20°C temperature range with the greatest day length. Bluegreens (Myxophyceae), on the other hand, grow best during the warmest part of the year and persist until temperature starts to drop off. Finally, the flagellated Cryptophyceae and Chrysophyceae attain their greatest biomass under ice cover.

Class succession patterns, however, are not ideal criteria upon which to analyze the adaptive nature of phytoplankton associations. While

to some extent members of a given algal Class share a common evolutionary history--that to some degree limits the adaptive range of a species--there are notable examples of wide-ranging adaptive characteristics of some Classes. Blue-green algae, for example, have been reported in dense concentration from hot springs to small ponds (Castenholz, 1967). A more fruitful approach might entail an examination of the morphological aspects of the changing species composition patterns.

For the purpose of discussion planktonic algae, their morphology can be divided into five groups: coccoid (unicellular forms), monad (motile, unicellular forms), colonial coccoid, colonial monad, and filamentous algae. In Lake Wingra, the principal groups are coccoid, monad, and colonial coccoid algae. The other two groups occur but not great enough to warrant a separation from the colonial coccoid classification. Within each of these categories, a further subdivision of size can be made. The classification of net plankton, nannoplankton, and ultraplankton has been a traditional one for the plankton as a whole (Strickland, 1960). Under these criteria, all organisms are classified by the maximum dimension of their particular morphology. Those cells or colony of cells whose maximum dimension exceeds 50 µm are placed in the net plankton category, those with maximum dimensions between 50 and 10 µm in the nannoplankton category, and those with maximum dimensions less than 10 µm in the ultraplankton category. In this study, I wish to depart from the traditional definitions of these categories and modify them to restrict the maximum dimension argument to cell size only and not to size of colony in which the cell resides.

The morphological variation of Lake Wingra phytoplankton has been summarized in Figures 9, 10, and 11. From these data and the associated environmental and biological data, some interesting conclusions can be drawn. The size distribution of phytoplankton species, for example (Fig. 9), indicates a shifting pattern of abundance of the three size class categories. In general, nannoplankton and ultraplankton dominate the phytoplankton during much of the year, especially during periods of nutrient depletion. The advantage of such a shift seems to be related to an adjustment of surface to volume ratios that allows for more efficient nutrient utilization at low concentrations (e.g., Munk and Riley, 1952; Eppley et al., 1969; and Corner and Davies, 1971). In those cases where net plankton is a large proportion of the phytoplankton in periods of nutrient deficiency (i.e., May to June), the species of net plankton are the large flagellates Ceratium hinundinella and Diplosalis acuta. These species of flagellates may be able to compensate for their large surface to volume ratio by their ability to move through the water--thus reducing the boundary layer limiting nutrient uptake. The importance of nannoplankton and ultraplankton, therefore, appears to be an adaptation to low nutrient levels encountered in the lake. When concentrations of nutrients are higher, net plankton organisms appear to grow better (cf. Wetzel, 1966; Maney, 1972).

Other than the period from May to June, there also appears to be a rather definite separation of motile and nonmotile phytoplankton species (Fig. 10). Although the reasons are not obvious for this temporal segregation, the general abundance of flagellated organisms during ice cover periods of the year appears to be a general rule (Wetzel, 1966; and Pechlaner, 1967). Motility is certainly an adaptive advantage in periods of ice cover when light intensity is low, and such an adaptation may explain the abundance of motile organisms during the winter months. Whatever the explanation, however, the apparent separation of motile and nonmotile phytoplankton species is a further confirmation of the adaptive nature of phytoplankton associations.

Perhaps the clearest indication of this adaptive nature is revealed in a colonial versus unicellular analysis of phytoplankton with time (Fig. 11). Colonial phytoplankton forms become most abundant from August to October, and the onset of their abundance corresponds to the maximum zooplankton standing crop observed in the lake (Teraguchi, 1969). This development of colonial biomass illustrates the optimization aspects of pattern formation in phytoplankton associations.

A rational interpretation of the abundance of colonial algal biomass might involve two basic processes--nutrient uptake and grazing by zooplankton. As previously stated, phytoplankton species with larger surface to volume ratios are at a competitive advantage during periods of low nutrient concentration (Dugdale, 1967). These same species, however, would also be subject to the most intense grazing pressure (Burns and Rigler, 1967; Nauwerck, 1963). It would appear reasonable, therefore, for those species with lower susceptibility to predation to accumulate more rapidly. Within the sheltered confines of a colony, however, low nutrient concentrations may yet exert an influence on the species, and the colonial species that do predominate are species with the smallest cells. Microcystis incerta, for example, is more abundant than Microcystis aeruginosa. In summary, the selection of species best adapted to particular nutrient supply and grazing regimes appears to be a real process. Similar patterns have been observed for a variety of other organisms (e.g., Lund, 1971; Dodson, 1970). Furthermore, the adaptive patterns observed appear to represent an optimization process within the phytoplankton association. Expressed through fecundity, this optimization process selects those species whose species' characteristics maximize growth rate against grazing losses.

The concept of optimality in biological processes is well established and finds expression in a wide variety of problems (cf. Rosen, 1967; Waterman and Morowitz, 1965). As Rosen indicates, the "Principle of Optimal Design" operates at two levels in biological systems: intrinsic and extrinsic. Intrinsic optimization is concerned with metabolic efficiencies. Ecological examples of intrinsic optimization would include observations on light and shade adapted species of planktonic diatoms (Talling, 1966; Jorgensen, 1969) and adaptations to temperature by planktonic diatoms (Jorgensen, 1968). Extrinsic optimizations relate

populations to specific environmental and biological variables--that is, to natural selection in an ecosystem.

Although such selection pressures have obvious implications for evolution of species, on a shorter time scale they also determine the species that become dominant in a given system. Rosen (1967) has summarized the qualitative effects of extrinsic optimization on the process of natural selection:

> The fundamental point to notice with regard to natural selection is that all types of competitive advantage, regardless of their initial nature, are ultimately translated into differences in fecundity . . . and it is these differences in fecundity which ultimately result in the predominance of the advantageous forms after a sufficient time has elapsed (p. 6).

He further qualifies these remarks to indicate a necessary assumption that the environment is held constant for a sufficient time. Because algal fecundity is directly translated into population biomass increments, Rosen's arguments concerning natural selection may easily be adapted to shorter time intervals in which species succession is the dominant mode of response. Under these conditions, extrinsic optimizations in an ecological unit result in the predominance of the species best adapted to the prevailing array of environmental and biological variables.

Application of optimization principles to phytoplankton associations is not without inherent difficulties. The chief obstacle to such applications may be the absence of sufficiently constant environmental conditions. Indeed, the bewildering diversity of planktonic organisms has been tied to the absence of equilibrium conditions (Hutchinson, 1961), and models incorporating the lack of equilibrium conditions have had some measure of success in simulating natural phytoplankton associations (Richerson, Armstrong, and Goldman, 1970). The absence of equilibrium conditions, however, only obscure optimization patterns and do not eliminate this process as a functional reality in natural phytoplankton associations. The appearance of optimization patterns in Lake Wingra, therefore, tend to support the validity of intrinsic and extrinsic optimization as functional concepts in this system.

Although the "Principle of Optimal Design" is useful in a qualitative evaluation of temporal and spatial variations in natural phytoplankton associations, its greatest value lies in its potential for quantifying these patterns. The application of optimality principles to phytoplankton associations is comparable to their use in engineering. Engineering applications traditionally include: (1) defining a set of competing solutions to a problem, (2) assigning a cost in mutually compatible

units to each of the solutions, and (3) selection of the optimal solution on a criterion of least cost (Rosen, 1967). In some cases the decision may be a bit more complex. Designing a bridge, for example, one would want to find an optimal design that would include maximum structural stability for the least expense.

In contrast to engineering applications, optimization analysis of phytoplankton would provide a framework within which to determine physiological capabilities most likely to yield the greatest biomass within a defined regime of biological and environmental variables. Each set of physiological capabilities available, as represented by an individual species, would have a growth rate associated with it. Physiological capabilities dealing with nutrient uptake, for example, would include variations in surface to volume ratios, colony formation, or motility. Extrinsic properties of the system, i.e., zooplankton density, turbulence, light, temperature, and nutrient availability, would enter the growth rate function variables. The species with the highest growth rate would then be considered to be the one that will produce the greatest biomass. Although the preceding example is simplistic in some ways, utilization of the principle in a dynamic model would allow one to deal explicitly with short term environmental fluctuations, which would affect the optimal physiological capabilities. Systematically employing realistic fluxes of nutrients, light, and other important variables, such a model would then provide a basis from which to forecast seasonal succession patterns. The ability to predict seasonal succession patterns, therefore, would directly aid management decisions regarding nutrient loading on or development of lake ecosystems.

In conclusion, application of optimization principles to studies of natural phytoplankton associations has potential to contribute both basic understanding and also to the development of sound management strategies to regulate nuisance phytoplankton communities. The current level of understanding of the factors that regulate phytoplankton succession patterns is largely based on results of correlation analyses between species appearance and various environmental variables (Wetzel, 1971). To be sure, there are more direct indications of controls and control mechanisms from sophisticated experimentation, but, in general, there exists no coherent body of theory that pulls all of the experimental and correlation data together. Such a body of theory, if developed, would significantly enhance our ability to deal with nuisance algal blooms, and thereby strengthen our management capability. Although this discussion may be short of developing such a body of theory, I do feel that significant advancement of our understanding of the complexity of natural phytoplankton associations will require the conceptual organization that optimization principles provide.

SECTION V

SEASONAL CHANGES IN THE ABUNDANCE OF PELAGIC-ZOOPLANKTON SPECIES IN LAKE WINGRA

Introduction

One of the major objectives to be carried out in this study is the quantification of the role of pelagic-zooplankton population in the transportation and transformation of energy and nutrients in Lake Wingra. Designing a study for this purpose requires certain strategy. Useful to the development of the strategy are previously acquired data on the abundance of pelagic-zooplankton species in Lake Wingra. These data can be used to determine which species, from a multitude of species, one must study in order to obtain a reasonable estimate of the role of the zooplankton population in nutrient and energy flows in Lake Wingra. This kind of determination is necessary, as it is practically impossible to study individually populations of all existing species. Also, these data can be used to select certain species populations so that the feeding spectra (herbivores or predators) ascribable to the total population are realistically represented by the selected few species. Finally, the information from these data can be used to develop a more optimal sampling design for future studies.

A literature review revealed that there is a lack of suitable, previously acquired data on the abundance of pelagic-zooplankton species in Lake Wingra. Tressler and Domogalla (1931) obtained data on seasonal changes in the abundance of various genera of pelagic zooplankton. Since their data were old and applicable only to genera, they would be of little use for the development of the necessary strategy.

We initiated, therefore, a study to characterize the seasonal changes in the abundance of pelagic-zooplankton species in Lake Wingra. Samples were collected systematically from July, 1968 to July, 1969. Analysis of the samples was completed in the spring of 1970.

Materials and Methods

Three sampling stations were established in Lake Wingra for the purpose of monitoring the seasonal change in the abundance of the pelagic-zooplankton species. These were located at the northeast, central, and southwest portions of the lake. Samples were taken at these stations (Fig. 14) at about two-week intervals during the ice-free period, about a week interval during the early part of the ice-cover period, and about four-week intervals during the latter part of the ice-cover period.

The cladocerans and copepods were sampled with a Clarke-Bumpus sampler (No. 10 netting) during the ice-free period and with a large Wisconsin

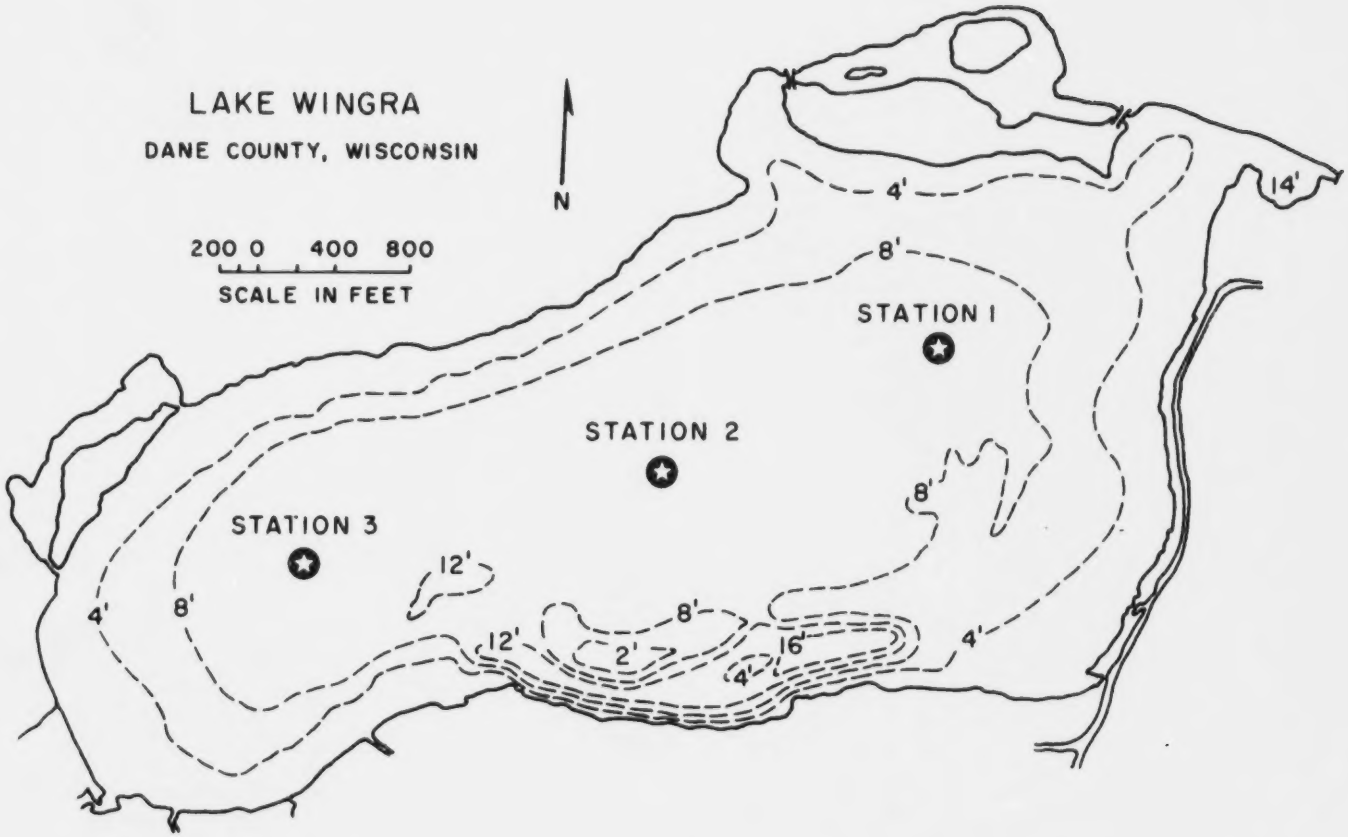

Figure 14. Contour map of Lake Wingra. The stations are indicated by crosses enclosed in circles.

net (No. 10 netting) during the ice-cover period. The C-B sampler was towed diagonally from near the bottom to the surface of lake in order to obtain a sample, whereas the Wisconsin net was towed vertically from near the bottom to the surface in order to collect a sample. Preliminary investigation indicated that the volume of water sampled during a two-minute diagonal tow with the C-B sampler was comparable to that sieved during a total vertical tow with the other net. During the ice-cover period, a large rectangular hole was cut in the ice so as to permit sampling. Triplicate samples were collected from each of the three stations at each sampling date. The samples were preserved in 5% formalin solution.

The rotifers were usually sampled with a 2 liter Van Dorn water bottle. On each sampling date, a sample was taken from 1, 2, and 2.75 m depths at each station. Each 2 liter sample was filtered through a No. 35 net to concentrate the organisms which were preserved in 5% formalin solution.

The cladoceran, copepod, and rotifer keys presented in the book edited by Edmondson (1959) were used for the identifications.

We used a subsampling technique to estimate the number of individuals of the various cladoceran and copepod species in each of the samples. Only 1 ml aliquot taken from each sample was used for the estimation. Statistical analysis (Ricker, 1938) revealed that random subsamples were usually taken from the samples under the imposed conditions of stirring of the samples. The estimates (number of individuals of the various species) of each set of triplicate samples was expressed at $\bar{x} \pm$ residual $(E(x-\bar{x})/N)$.

We made total counts of the individuals of the various species of rotifers in each of the samples. The organisms in each sample were concentrated with a small funnel (No. 35 netting), having a small opening at the apex which was closed. The organisms were then placed in a small chamber, and the total numbers of individuals of the various species were counted. As the counts of the individuals of the various species in the samples taken from 1, 2, and 2.75 m were fairly comparable on many sampling dates, we pooled the three sets of counts to derive the mean value and residuals for each sampling date.

A settling technique was used to determine the volume (or standing crop) of the pelagic zooplankters in each of the three samples taken on each of the sampling dates. A mean volume was computed for each set of samples.

Light penetration and vertical temperature profiles were determined on each sampling date, whereas the oxygen profile was usually determined on every other sampling date of the ice-free period and on every sampling date of the ice-cover period. Light penetration was determined with a Secchi disc, while temperature profile was determined with a

thermistor. A modified Winkler Method was used to measure oxygen content of the water samples.

Results

CLADOCERANS

Eighteen species of cladocerans were identified from plankton samples taken from the open-region of Lake Wingra (Table 2). On the basis of our method of estimation (involving subsampling of the samples), the numbers of individuals of ten of these species could not be quantified from the samples taken throughout the one-year period. These ten species were Acroperus harpae, Camptocercus macrurus, Ceriodaphnia megalops, Ceriodaphnia reticula, Chydorus ovalis, Eurycerus lamellatus, Macrothrix rosea, Pleuroxus denticulatus, Scapholeberis kingi, and Simocephalus serrulatus. The individuals of the other seven species occurred in adequate numbers for at least certain times of the year.

Alona quadrangularis

This species was present for only a very short period during the year (Fig. 15). During the period of occurrence (primarily the month of November), the estimated mean number of individuals of Alona quadrangularis never exceeded about 1500 per 660 liters. For any given date of occurrence, the number of individuals at the three stations differed somewhat; this was probably an artifact resulting from the use of subsampling technique for estimation when very few individuals of this species were present in the samples.

Bosmina longirostris

The seasonal trends in the abundance of this species at the three sampling stations were very similar (Fig. 16). The density of Bosmina longirostris was lowest during the summer (estimated mean counts ranged from zero to about 1300 individuals per 660 liters), intermediate for sampling dates during autumn and spring (estimated mean counts ranged from about 5000 to about 16,000 individuals per 660 liters) and maximum during autumn and spring (estimated mean counts ranged from about 45,000 to about 100,000 individuals per 660 liters during the period which included sampling dates of 10 October, 24 October, and 7 November 1968, and ranged from about 50,000 to 220,000 individuals per 660 liters during the period which included sampling dates of 22 April, 6 May, 23 May, and 6 June 1969). The periods of maximum density were preceded by a sharp increase in numbers and followed by a sharp decrease in numbers.

On many of the sampling dates, the mean estimated densities of this species at the three stations were fairly comparable (Fig. 16).

Table 2. Species of cladocerans, copepods, and rotifers found in the samples taken from the open-water region of Lake Wingra during 1968 and 1969.

Cladocera

Acroperus harpae

Alona quadrangularis

Bosmina longirostris

Camptocercus macrurus

Ceriodaphnia megalops

Ceriodaphnia quadrangula

Ceriodaphnia reticula

Cydorus sphaericus

Cydorus ovalis

Daphnia galeata

Daphnia retrocurva

Diaphanosoma brachyurum

Eurycerus lamellatus

Leptodora kindtii

Macrothrix rosea

Pleuroxus denticulatus

Scapholeberis kingi

Simocephalus serrulatus

Copepods

Cyclops bicuspidatus thomasi

Diaptomus siciloides

Eucyclops agilus

Mesocyclops edax

Rotifera

Asplanchna priodonta

Brachionus angularis

Brachionus calyciflorus

Filinia opoliensis

Keratella cochlearis

Keratella quadrata

Monostyla quadrindentata

Notholca acuminata

Polyarthra suryptern

Polyarthra vulguris

Synchaeta oblonga

Voronkowia mirabilis

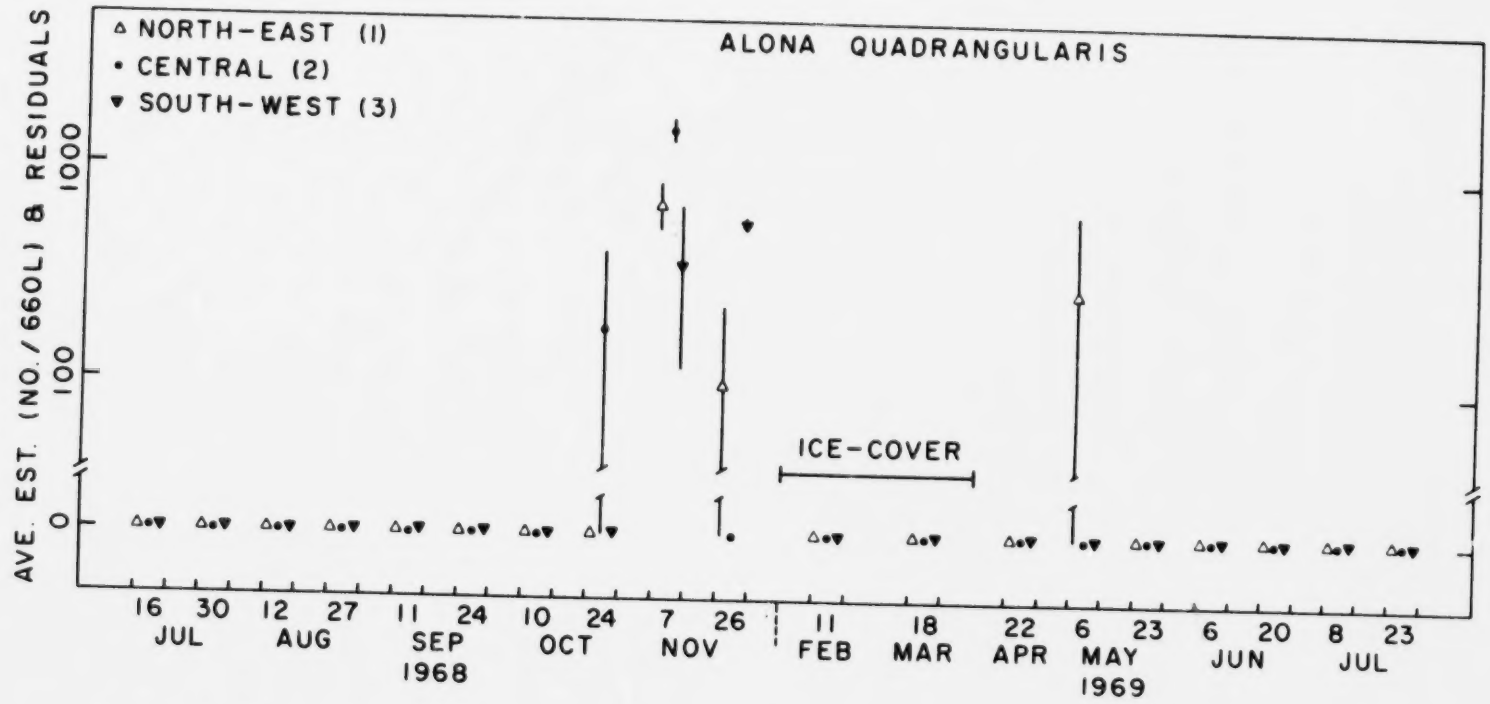
△ NORTH-EAST (1)
• CENTRAL (2)
▼ SOUTH-WEST (3)
ALONA QUADRANGULARIS
AVE. EST. (NO./66OL) & RESIDUALS
1000
100
0
ICE-COVER
16 30 12 27 11 24 10 24 7 26 11 18 22 6 23 6 20 8 23
JUL AUG SEP OCT NOV FEB MAR APR MAY JUN JUL
1968
1969

Figure 15. Seasonal changes in the abundance of Alona quadrangularis in Lake Wingra.

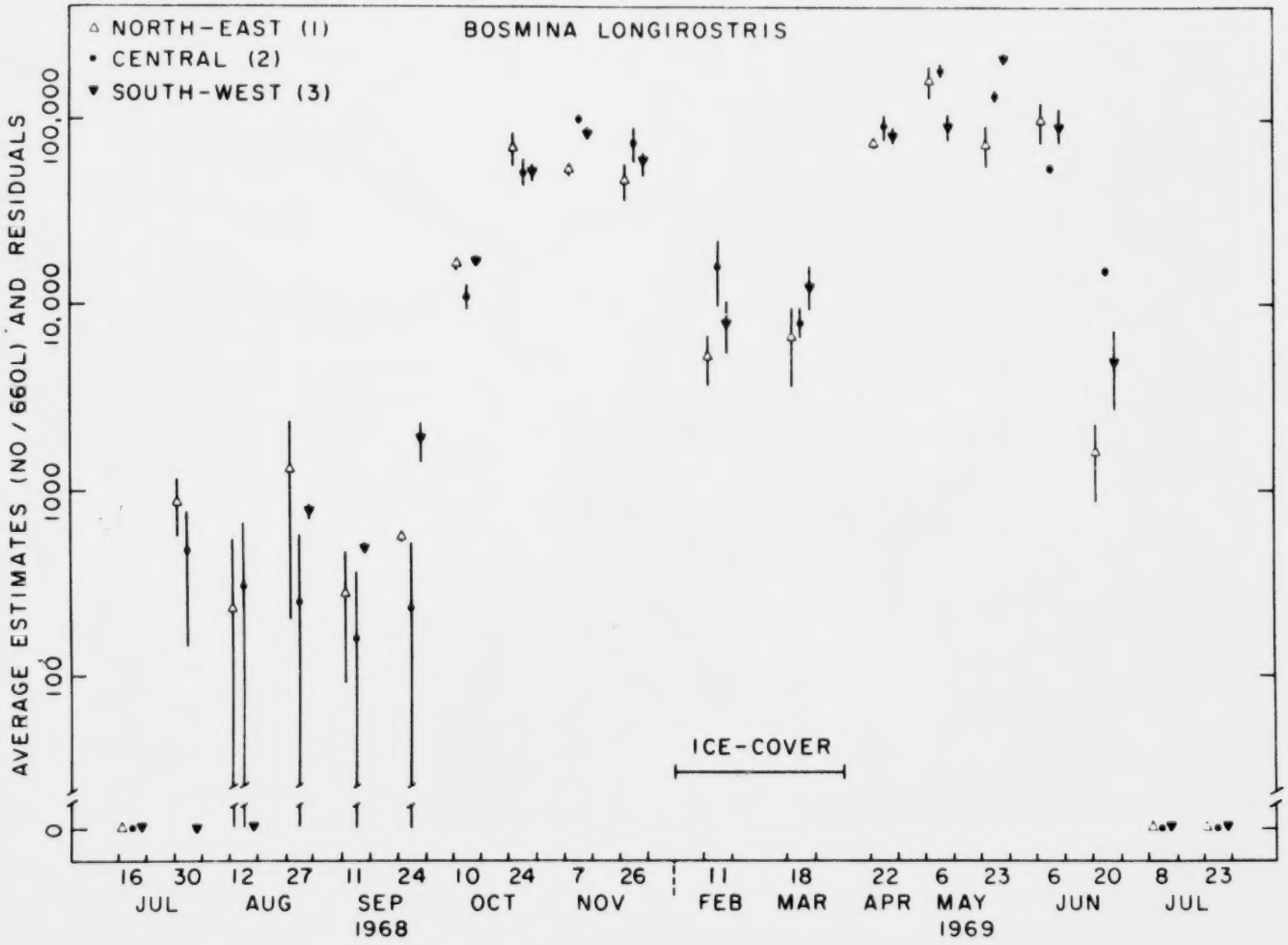

Figure 16. Seasonal changes in the abundance of Bosmina longirostris in Lake Wingra.

Ceriodaphnia quadrangula

This cladoceran species was present in the open-water region of Lake Wingra only during late spring, summer, and autumn (Fig. 17). From 16 July to 7 November 1968, there was a steady decline in the number of individuals. The mean number of individuals ranged from about 6,000 to 13,000 per 660 liters on 16 July and from about 500 to 3,500 on 7 November. This gradual decline in mean numbers was followed by a sharp decrease in numbers. The estimated mean count of this species per 660 liters was zero at all stations on 26 November 1968, 11 February 1969, 18 March 1969, and 22 April 1969. From 6 May to 20 June, there was a sharp increase in the number of individuals. This period of rapid increase in numbers of individuals was followed by a period (includes sampling dates of 20 June, 8 July, 25 July 1969) during which the average density of this species ranged from about 70,000 to 150,000 individuals per 660 liters.

The average densities of this species at the three stations were quite different on many of the sampling dates in 1968, but were quite similar on many of the sampling dates in 1969.

Chydorus sphaericus

This species was most abundant during spring, summer, and autumn (Fig. 18). The maximum average density observed during these periods was about 30,000 individuals per 660 liters, and the minimum density was about 2,500 individuals per 660 liters. There was a sharp decline in the numbers of individuals prior to ice-cover and a sharp increase in numbers shortly after termination of ice-cover.

The mean densities of Chydorus at the three stations were similar only for some sampling dates.

Daphnia galeata

The estimated mean numbers of this species per 660 liters was highest during the summer (up to about 150,000 per 660 liters), intermediate (up to about 70,000 per 660 liters) during the autumn, and lowest (up to about 40,000 per 660 liters) during the winter and early spring (Fig. 19). Most of the estimated mean values for summer sampling dates were within the range of about 50,000 to about 130,000 individuals per 660 liters. Most of the estimated mean values for the autumn sampling dates were within the range of about 20,000 to about 50,000 individuals per 660 liters. Most of the estimated mean values for the winter and early spring sampling dates were within the range of about 2,000 to 3,000 individuals per 660 liters.

On most of the sampling dates, the estimated mean values for the three stations were remarkably similar.

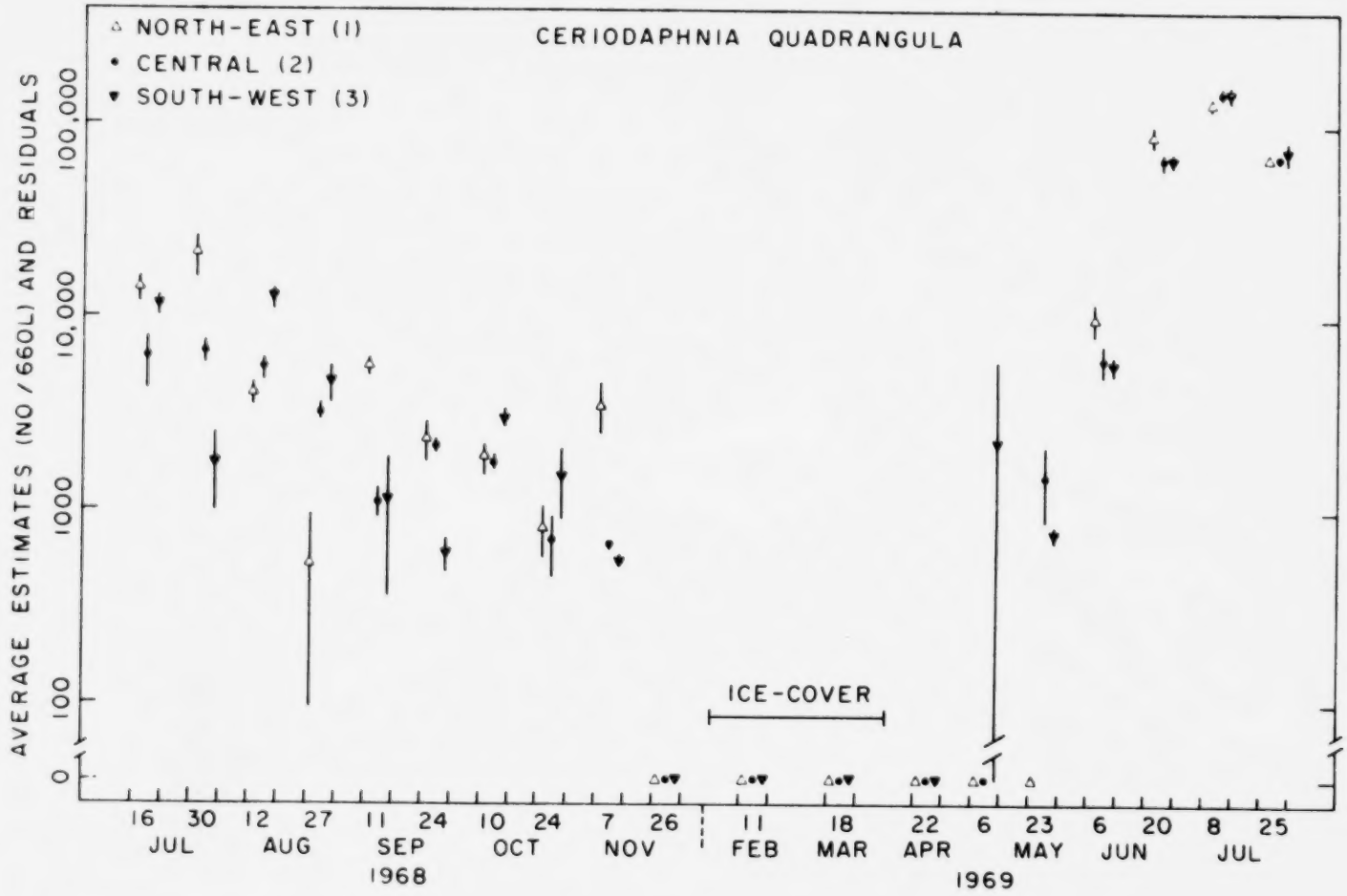

Figure 17. Seasonal changes in the abundance of Ceriodaphnia quadrangula in Lake Wingra.

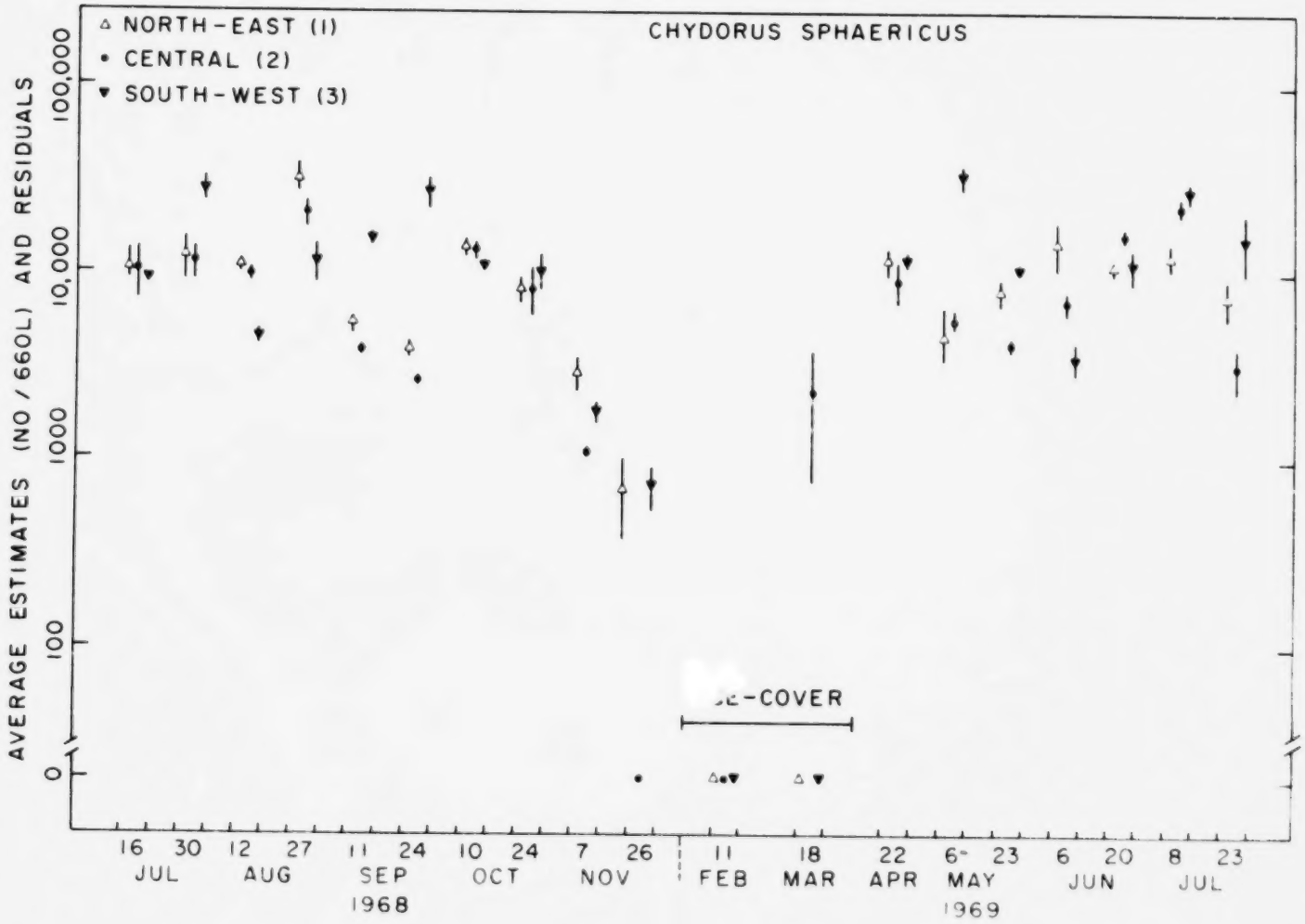

Figure 18. Seasonal changes in the abundance of Chydorus sphaericus in Lake Wingra.

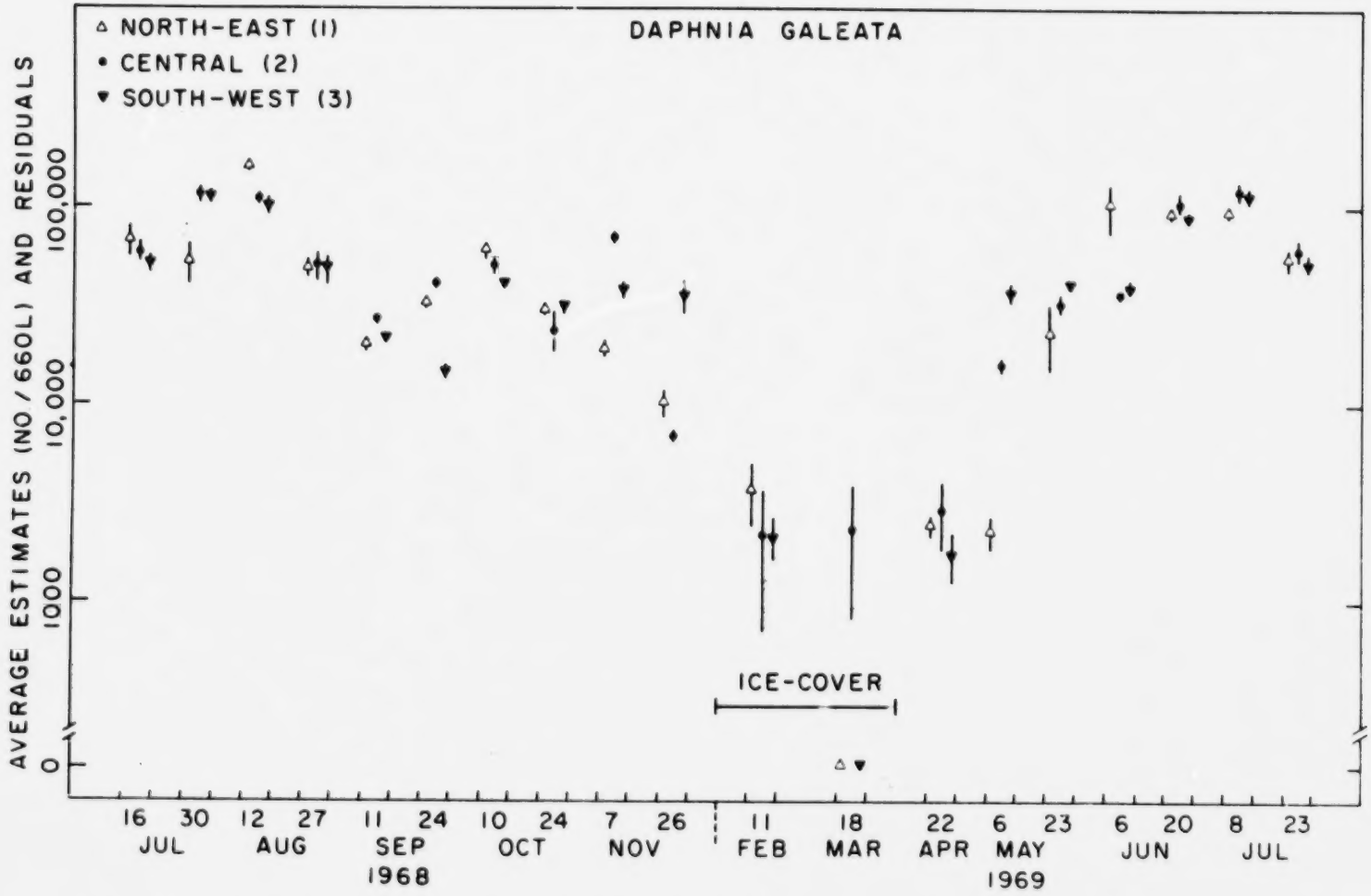

Figure 19. Seasonal changes in the abundance of Daphnia galeata in Lake Wingra.

Daphnia retrocurva

The seasonal trend in the abundance of this species was very similar to the seasonal trend in the abundance of Daphnia galeata (Figs. 19 and 20). Daphnia galeata was most abundant during the summer, intermediately abundant in the autumn, and least abundant in the winter and early spring (Fig. 20). Generally, the ranges within which most of estimated values for the summer and autumn sampling dates occurred were about 50,000 to about 150,000 individuals per 660 liters and about 5,000 to about 40,000 individuals per 660 liters. Estimated numbers of individuals per 660 liters for winter and early spring sampling dates were usually zero.

On many of the sampling dates, the estimated values for the three stations were quite similar.

Diaphanosoma brachyarum

This species occurred only during the summer and early autumn (Fig. 21). During the early summer, there was a rapid increase in the numbers of these organisms. From 20 June 1969 to 25 July 1969, the estimated values changed from zero to about 50,000 to 100,000 individuals per 660 liters. Maximum abundance occurred during July and August; most of the values observed were within the range of about 30,000 to 80,000 individuals per 660 liters. From 11 September 1968 to 24 October 1968, the estimated values changed from about 35,000 - 60,000 to zero individuals per 660 liters.

On most of the sampling dates, the estimated mean values for the three stations were very similar.

Leptodora kindtii

This species occurred only for a short period (July to early part of August) (Fig. 22). Most of the estimated mean values were in the range of about 500 to 1,000 individuals per 660 liters for 30 July and 12 August 1969 and in the range of about 2,000 to 5,000 for 8 July and 25 July 1969.

On most of the sampling dates on which this species was present, the values for the three stations were reasonably comparable.

COPEPODS

Four species of copepods (three cyclopoids and one calanoid) were identified from samples collected from the open-water region of Lake Wingra during 1968 and 1969 (Table 2). Cyclops bicuspidatus thomasi, Diaptomus

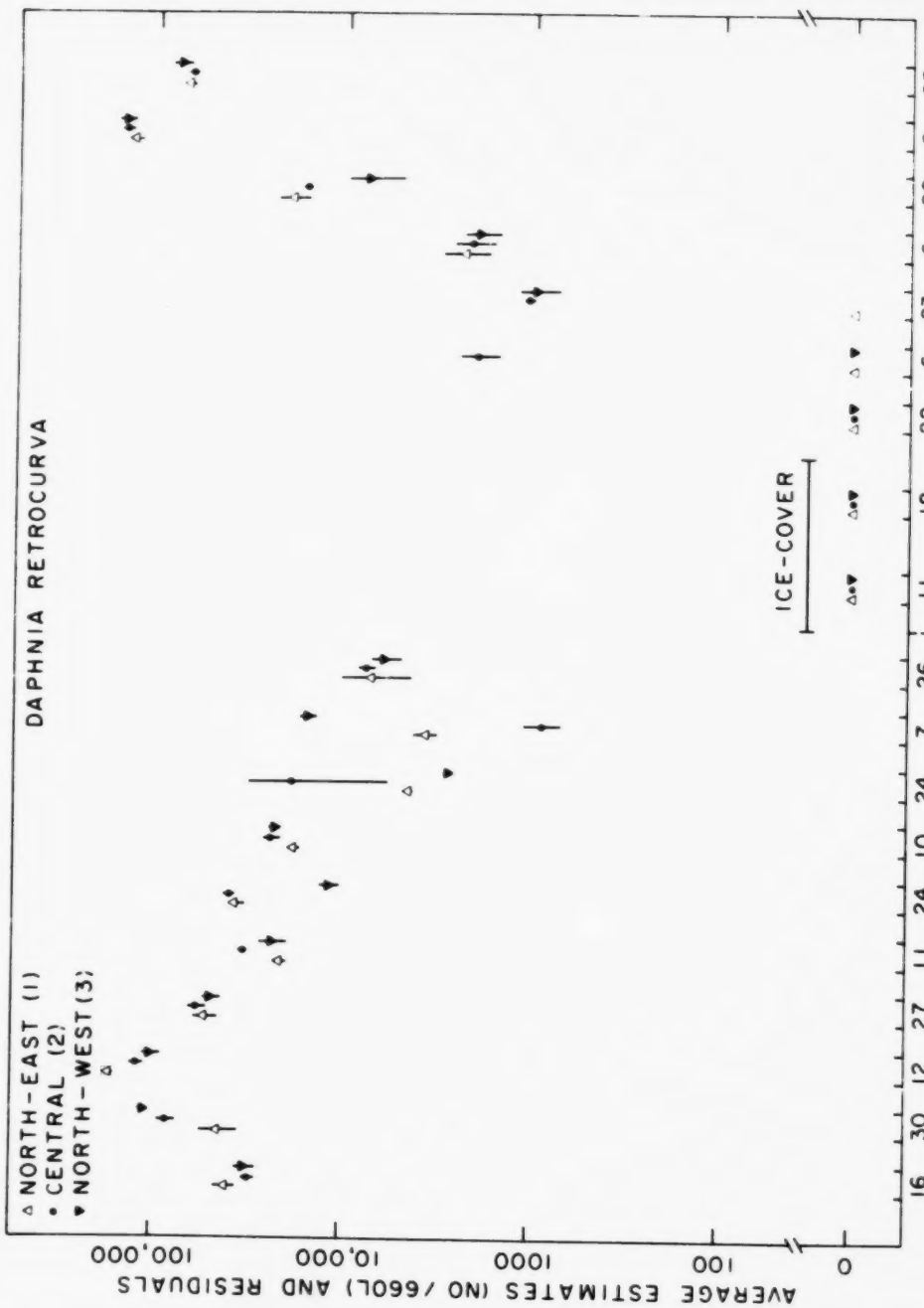

Figure 20. Seasonal changes in the abundance of Daphnia retrocurva in Lake Wingra.

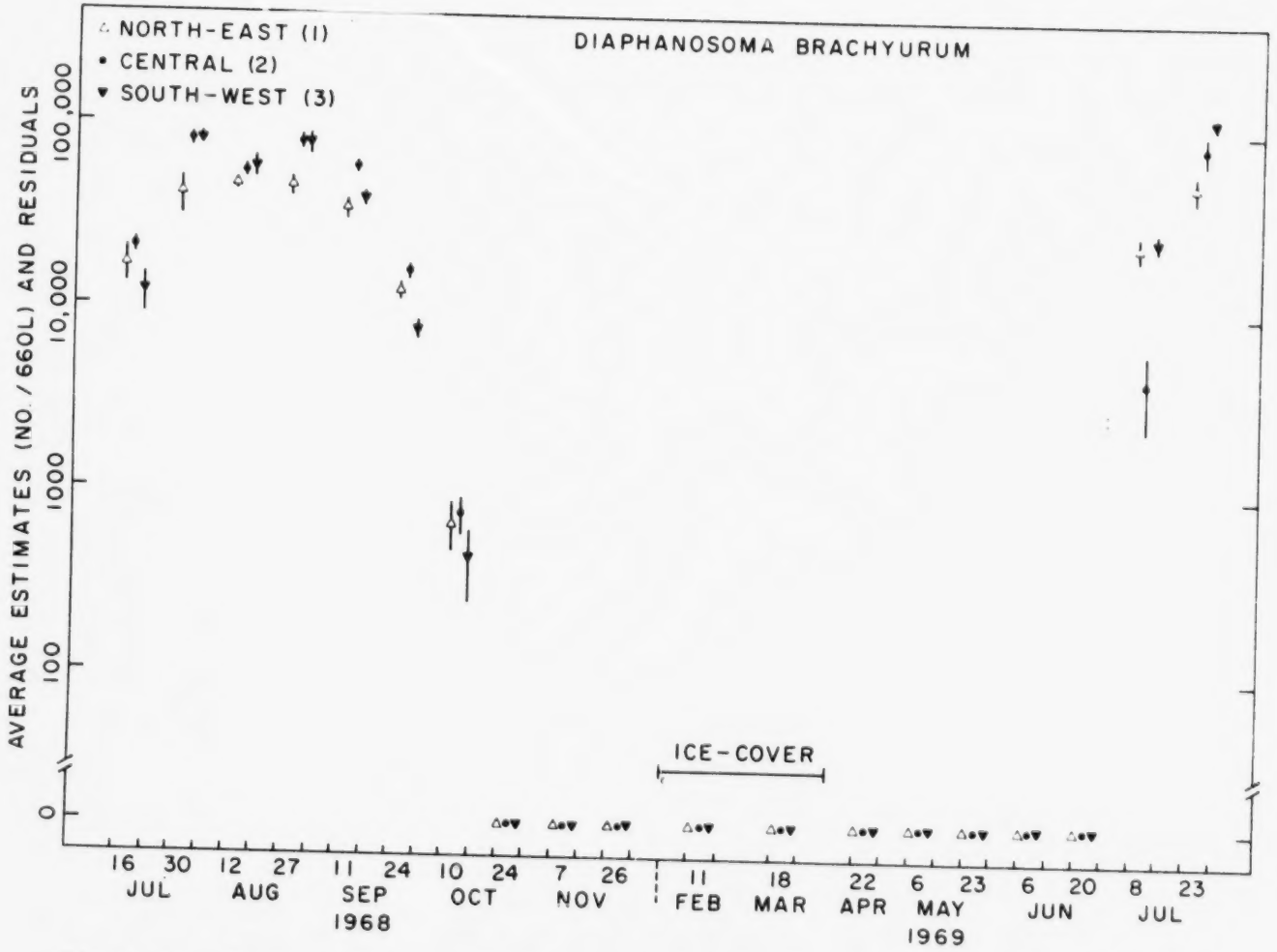

Figure 21. Seasonal changes in the abundance of Diaphanosoma brachyurum in Lake Wingra.

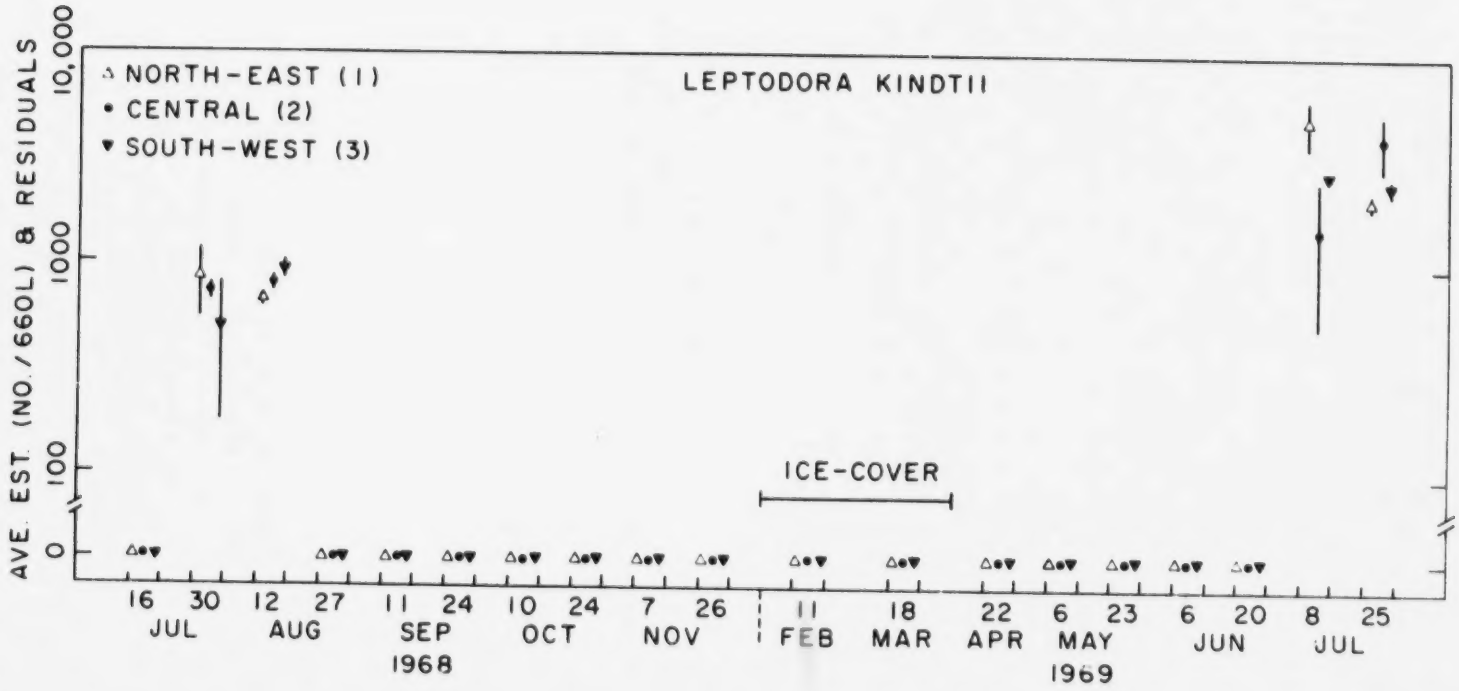

Figure 22. Seasonal changes in the abundance of Leptodora kindtii in Lake Wingra.

siciloides, and Mesocyclops edax were abundant enough throughout the year so that the seasonal change in their abundance could be characterized reasonably well.

Cyclops bicuspidatus thomasi

This species was present in adequate numbers throughout the year (Fig. 23). Throughout the summer, their abundance seemed to remain about 10,000 to 30,000 individuals per 660 liters. There was a fairly sharp decline in the mean estimated abundance during the autumn of 1968; during this period the mean abundance changed from 15,000 - 25,000 individuals per 660 liters to 1,300 - 3,000 individuals per 660 liters. Maximum mean abundance occurred during the winter and early spring; most of the values were within the range of 30,000 to 100,000 individuals per 660 liters. There was a sharp decline in numbers during the late spring as the mean estimated numbers changed from a range of 30,000 to 100,000 individuals per 660 liters to a range of about 3,000 to 5,000 individuals per 660 liters. From 20 June to 8 July 1969, there appeared to be another sharp increase in abundance.
On most of the sampling dates, the mean estimated abundance for the three stations were very similar.

Diaptomus siciloides

The seasonal trend in the abundance of this species involved only minor fluctuations in abundance throughout the year (Fig. 24). Throughout the summer and autumn of 1968 and winter of 1969, the density of this species appeared to fluctuate within the range of about 20,000 to 70,000 individuals per 660 liters. From 22 April to 6 June, there seemed to be a gradual increase in the numbers of this organism. During the period including 20 June, 8 July, and 25 July 1969, the density of this species was in the range of about 50,000 to 100,000 individuals per 660 liters.

Again, on most of the sampling dates, the numbers of this species at the three stations were very comparable.

Mesocyclops edax

This cyclopoid copepod appeared to occur only during the summer (Fig. 25). Its abundance on the various sampling dates in the summer of 1968 ranged for the most part from 3,000 to 10,000 individuals per 660 liters. Its abundance on the various sampling dates in the early summer of 1969 ranged generally, however, from 15,000 to 30,000 individuals per 660 liters.

Only on some of the sampling dates on which this species occurred did the numbers of this organism at the three stations appear comparable.

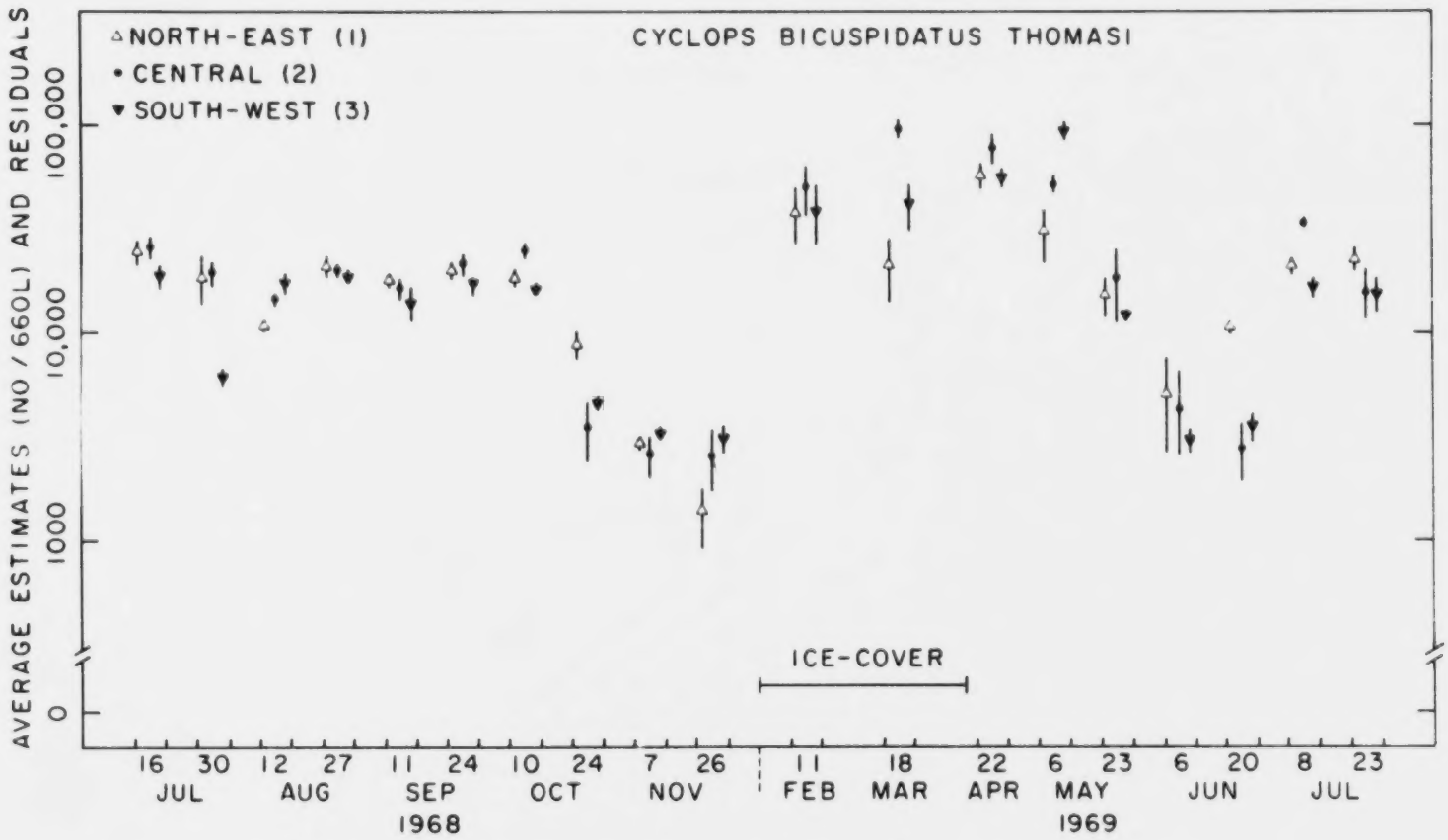

Figure 23. Seasonal changes in the abundance of Cyclops bicuspidatus thomasi in Lake Wingra.

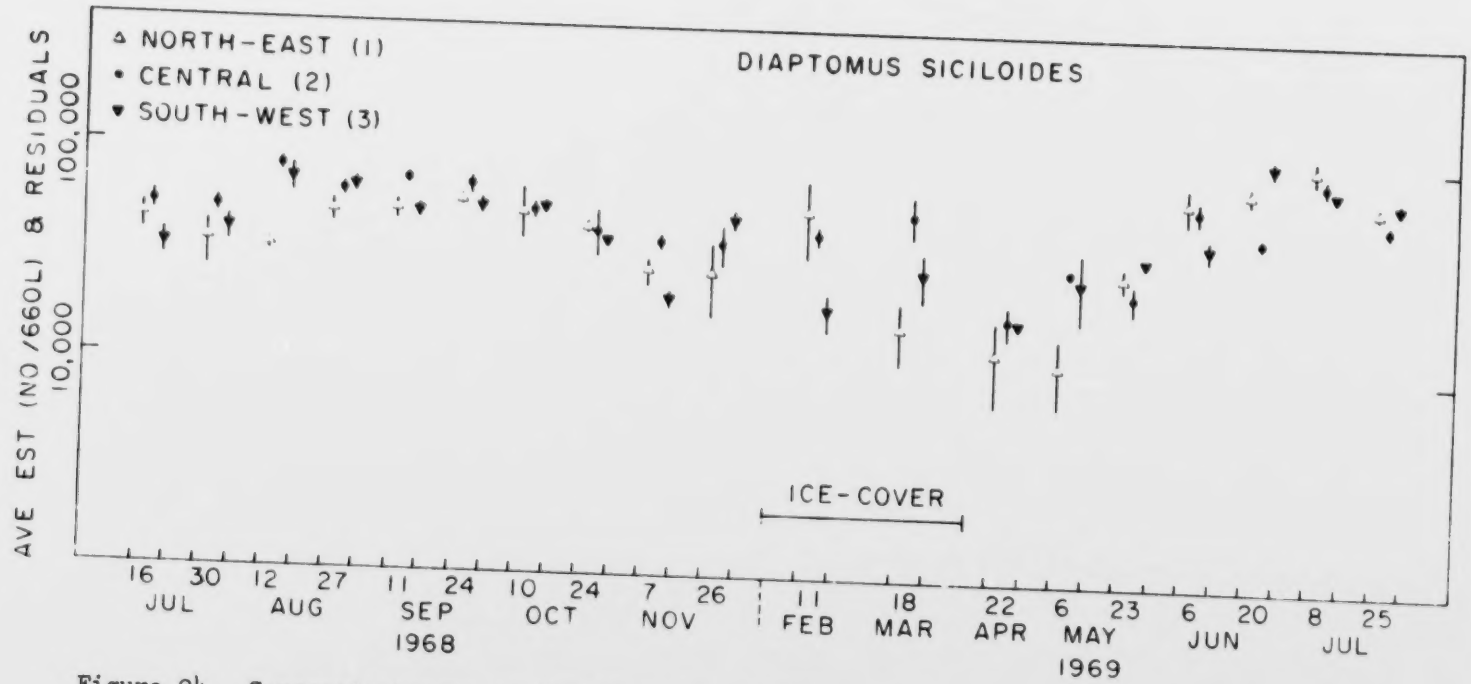
NORTH-EAST (1)
CENTRAL (2)
SOUTH-WEST (3)
DIAPTOMUS SICILOIDES
AVE EST (NO/660L) & RESIDUALS
100,000
10,000
ICE-COVER
16 30 12 27 11 24 10 24 7 26 11 18 22 6 23 6 20 8 25
JUL AUG SEP OCT NOV FEB MAR APR MAY JUN JUL
1968
1969

Figure 24. Seasonal changes in the abundance of Diaptomus siciloides in Lake Wingra.

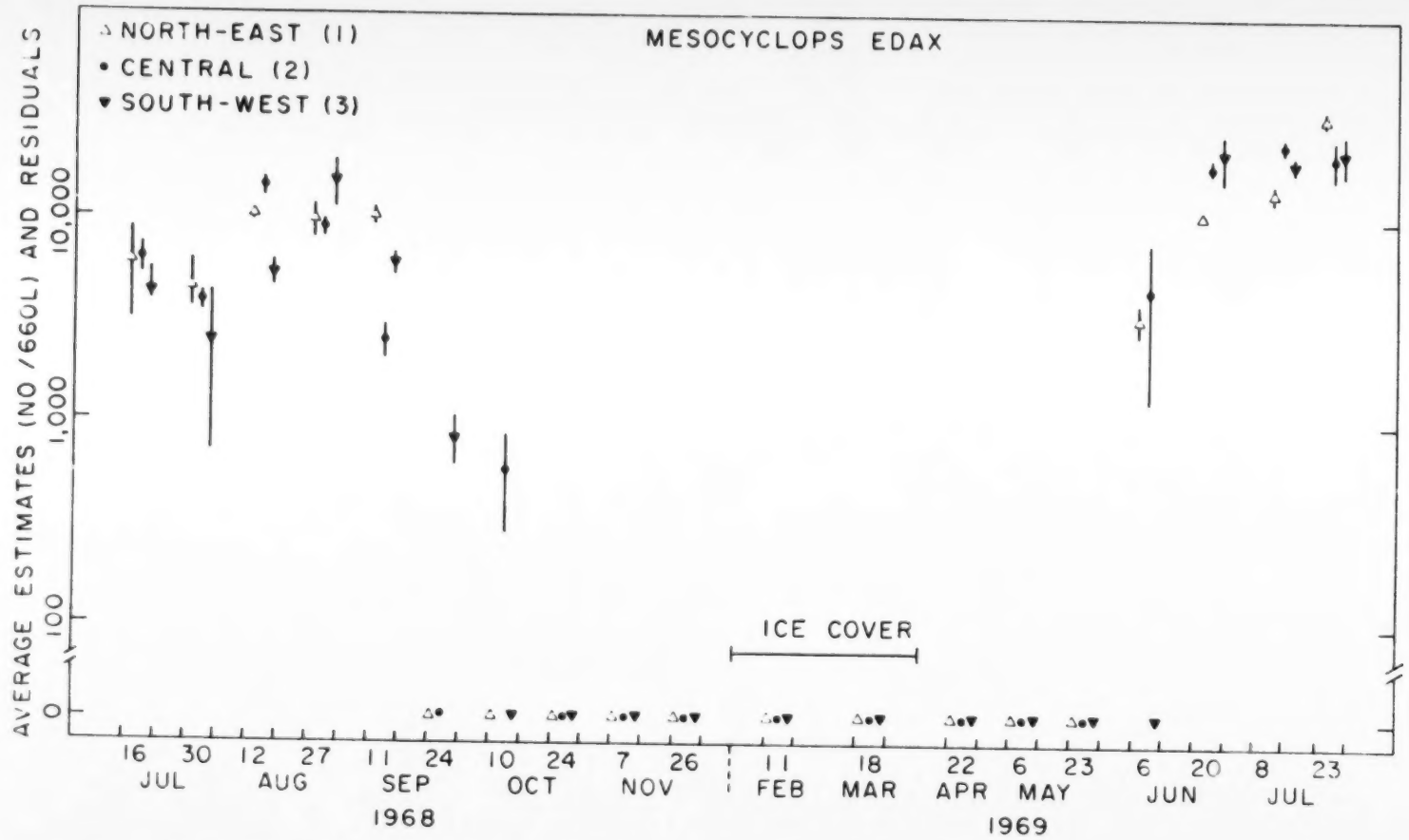

Figure 25. Seasonal changes in the abundance of Mesocyclops edax in Lake Wingra.

ROTIFERS

Twelve species of rotifers were identified from the samples collected from the open-water region of Lake Wingra during 1968 and 1969 (Table 2). Since Keratella quadrata, Monostyla quadridenta, Notholca acuminata, Synchaeta oblonga, and Voronkowia mirabilis did not occur in adequate numbers on most of the sampling dates, we were not able to characterize reliably the seasonal change in their abundances.

Asplanchna priodonta

This species had only one major peak of abundance during the year (Fig. 26). From 11 February to 6 May 1969, the average density of this organism changed from virtually no individuals per 2 liters to at least 20 individuals per 2 liters. From 6 May to 6 June 1969, there was a very rapid decline in the density of this species. On most of the other sampling dates, this species was not present.

The variation in the average densities of this species at the three stations for most of the sampling dates did not appear to be significant.

Brachionus angularis

This species was most abundant during the summer and late spring (Fig. 26). From 16 July to 27 August 1968, the average density of this species changed from practically no individuals per 2 liters to at least 20 individuals per 2 liters. From 27 August to 24 September 1968, the average density changed from at least 20 individuals per 2 liters to no individuals. Between 24 September to 26 November 1968, this species was absent except on one sampling date. There appeared to be an increase in the numbers of individuals from 26 November to 18 March 1969 and a decrease in the numbers of individuals from 18 March to 22 April 1969. Only on one sampling date (8 July) in the spring and summer of 1969 did this species occur in reasonable numbers.

The densities of this organism at the three stations were similar on many of the sampling dates.

Brachionus calyciflorus

This species was present only during late winter and early spring (Fig. 26). However, the average numbers of individuals of this species never exceeded 18 individuals per 2 liters.

Keratella cochlearis

This species was present on all the sampling dates at least at two of the

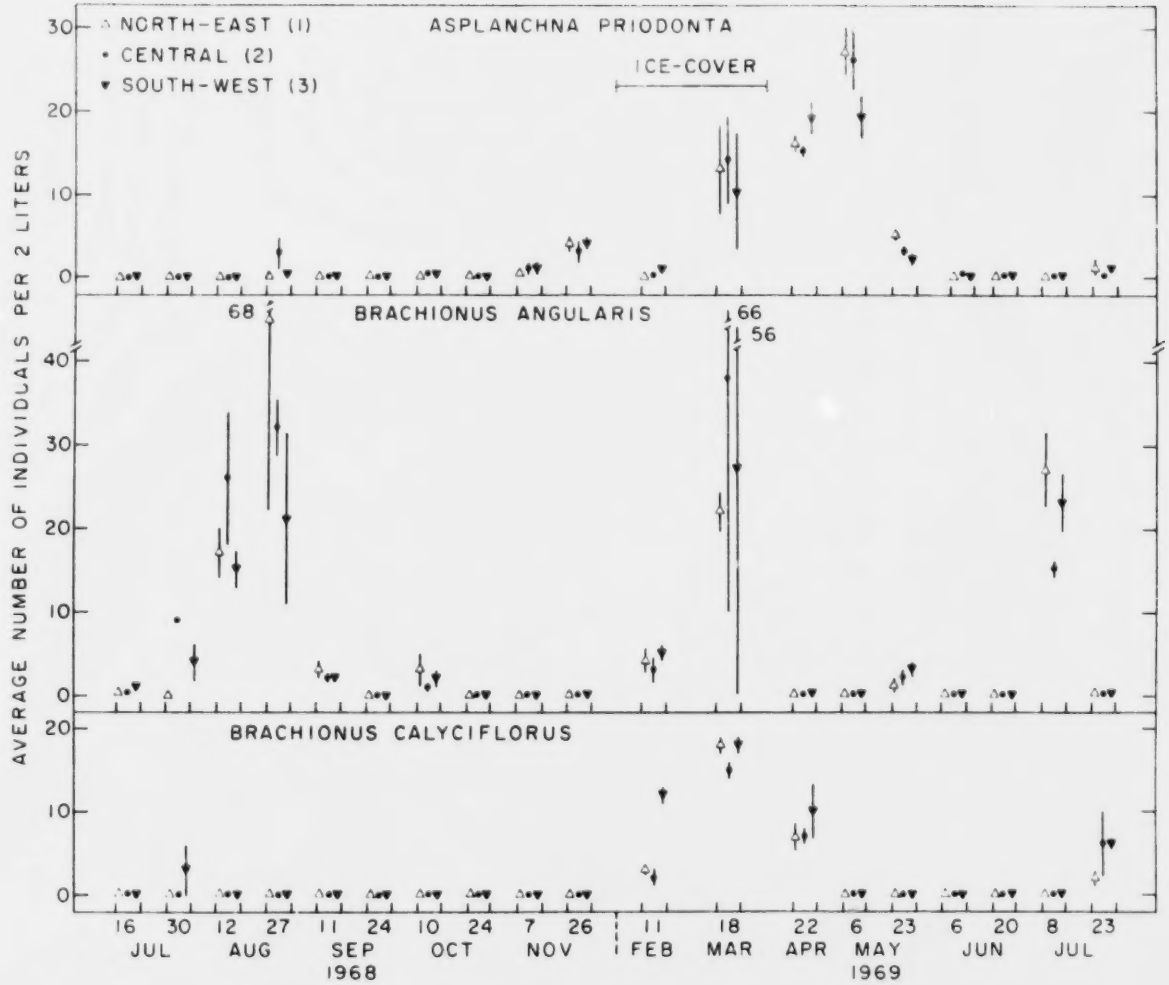

Figure 26. Seasonal changes in the abundance of Asplanchna priodonta, Brachionus angularis, and Brachionus calyciflorus in Lake Wingra.

three sampling stations (Fig. 27). A large increase in abundance occurred during the period from 16 July to 30 July 1968; the average numbers of individuals per 2 liters ranged from 22 to 25 on the former sampling date and from 55 to 108 on the latter. A large decrease in abundance took place during the period from 30 July to 27 August 1968; the average number of individuals per 2 liter ranged from 55 to 108 on the former date and from 3 to 14 on the latter date. On the subsequent three sampling dates, the density never exceeded 10 individuals per 2 liters. A moderate increase in abundance occurred in October 1968; as the average number of individuals per 2 liters changed from a maximum of 9 on 10 October to a minimum of 21 on 24 October. The average density ranged from 20 - 25 individuals per 2 liters on the sampling dates of November 1968. From 18 March to 23 May 1969, the average density changed from a minimum of 71 individuals per 2 liters to a maximum of 2 individuals per 2 liters. On the sampling dates of June and July 1969, the average density never exceeded 17 individuals per 2 liters.

On most of the sampling dates, the average densities at the three stations were remarkably similar.

Polyarthra eurypterus

This species was present in low numbers mostly during the late summer and autumn (Fig. 28). The density never exceeded 9 individuals per 2 liters.

Polyarthra vulgaris

This species occurred in varying numbers throughout the year (Fig. 28). From 12 August to 7 November 1968, there appeared to be a gradual increase in the numbers of individuals of this species. During this period the average density changed from about 1 to a maximum of 39 individuals per 2 liters. There was a decrease in the numbers of individuals from 7 November 1968 to 11 February 1969. On most of the sampling dates in the spring and early summer of 1969, the average density rarely exceeded 10 individuals per 2 liters.

Tetra mastix (= Filinia) opoliensis

The seasonal trend in the abundance of this species consisted of high density during the early part of the summer and very low density during the other seasons (Fig. 28). Maximum average density was 32 individuals per 2 liters on 30 July 1968 and 57 individuals per 2 liters on 8 July 1969. On most of the other sampling dates, the average density at the three stations rarely exceeded 5 individuals per 2 liters.

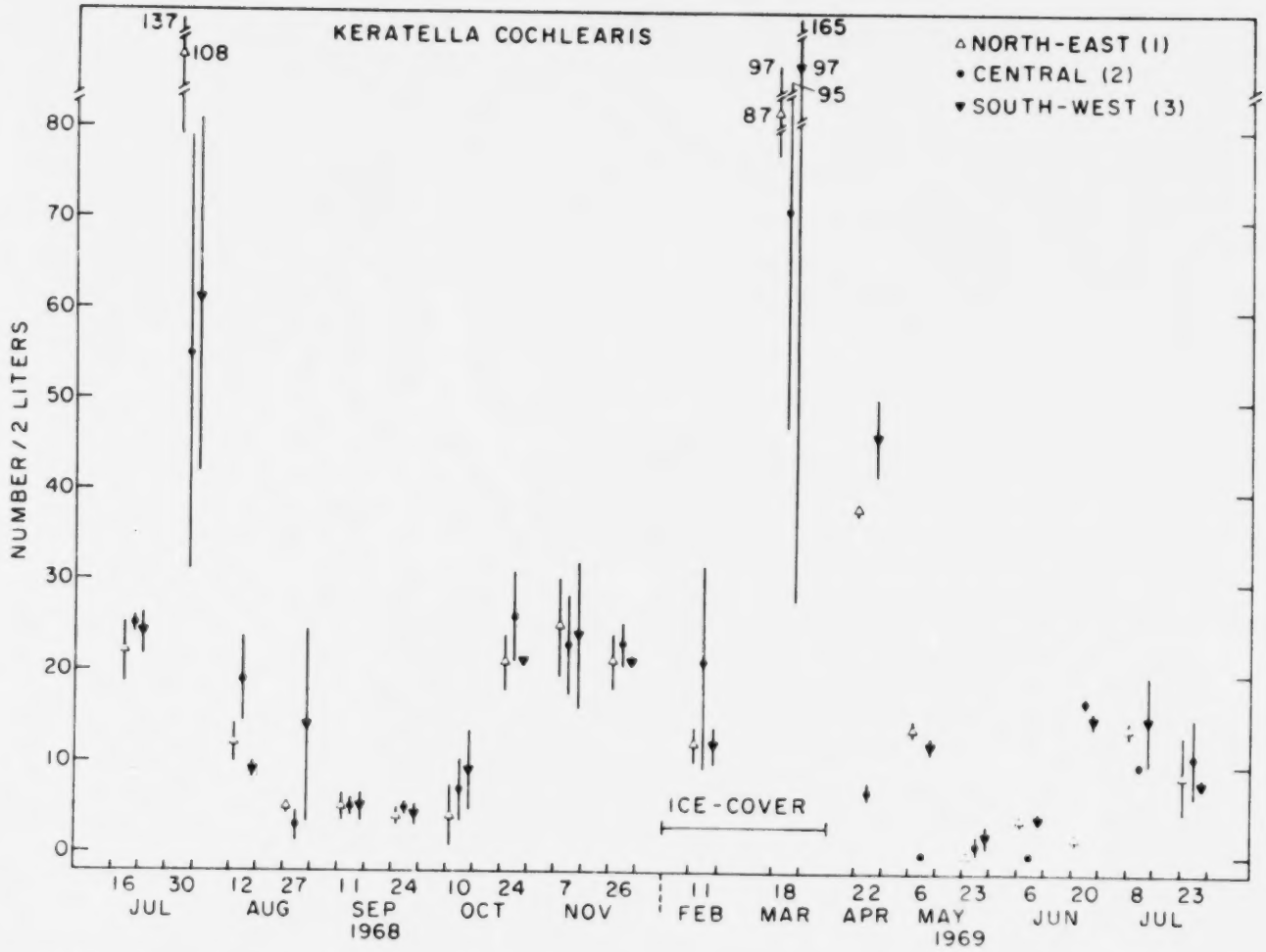

Figure 27. Seasonal changes in the abundance of Keratella cochlearis in Lake Wingra.

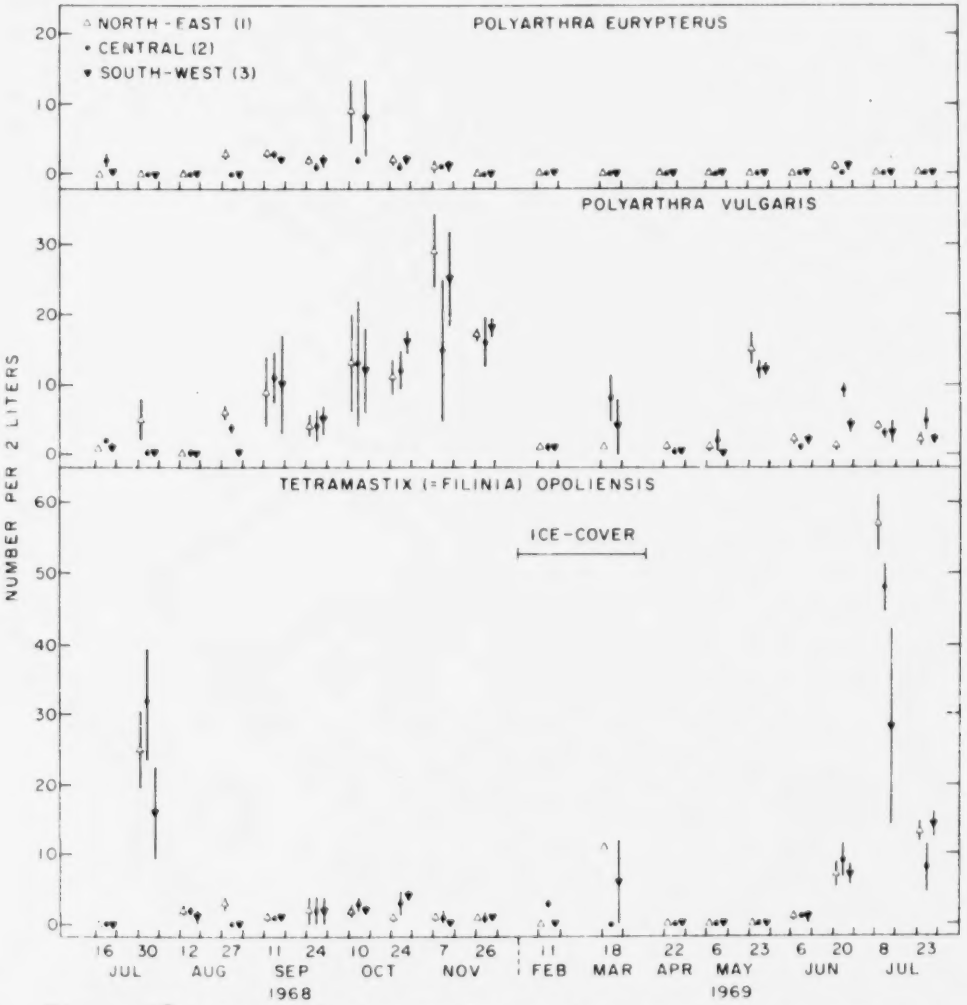

Figure 28. Seasonal changes in the abundance of Polyarthra eurypterus, Polyarthra vulgaris, and Tetramastix opoliensis in Lake Wingra.

Standing Crop of Pelagic Zooplankton

Not more than a 2.5 fold change in the volume of pelagic zooplankton occurred during the sampling period (Fig. 29). Greatest average volume was recorded during the summer (32 to 34 cc per 660 liters on 12 August 1968 and 33- 36 cc per 660 liters on 8 July 1969), whereas the least average volume was observed during the ice-cover period (6 - 9 cc per 660 liters on 11 February 1969 and 4.5 - 12 cc per 660 liters on 8 March 1969). The seasonal trend in the volume of pelagic zooplankton seemed to consist of a sharp increase from 16 July to 12 August 1969, a sharp decrease from 12 August to 11 September 1968, a very gradual decrease from 11 September to at least 26 November, an increase from 8 March to 6 May 1969, a slight decrease from 6 May to 6 June 1969, and a pronounced increase from 6 June to 8 July 1969.

There seemed to be a reasonable correlation between the average volume of zooplankton and average water temperature (Fig. 30). The only sets of data which did not fit reasonably well were those obtained for 12 August 1968 and 20 June 1969. Nevertheless, it seems that temperature might be a good characteristic to use for the prediction of the volume of pelagic zooplankton up to about 30 cc per 660 liters.

Discussion

CLADOCERANS

Of the cladoceran species, Acroperus harpae, Camptocercus macrurus, Ceriodaphnia megalops, Ceriodaphnia reticula, Cydorus ovalis, Eurycercus lamellatus, Macrothrix rosea, Pleuroxus denticulatus, Scapholeberis kingi, and Simocephalus serrulatus are present in such low numbers that they are definitely not worth consideration in subsequent, detailed studies.

Alona quadrangularis and Leptodora kindtii are probably not worth consideration. Alona occurs only for a short time and never exceeds densities of about 1500 per 660 liters (Fig. 15). Leptodora kindtii occurs for a short time (probably not more than a month period), but can reach densities as high as 50,000 per 660 liters (Fig. 22). In spite of this fairly high density, Leptodora kindtii does not seem to have an obvious effect on the various cladoceran species (also copepod species). During the period when Leptodora is most abundant, there is no corresponding decrease in density of the various cladoceran and copepod species (See Figs. 15 to 25). Wright (1965), studying the population dynamics and production of Daphnia in Canyon Ferry Reservoir, observed density decrease of Daphnia during peak abundance of Leptodora. This correspondence is not obvious in Lake Wingra because Leptodora feeds probably on several

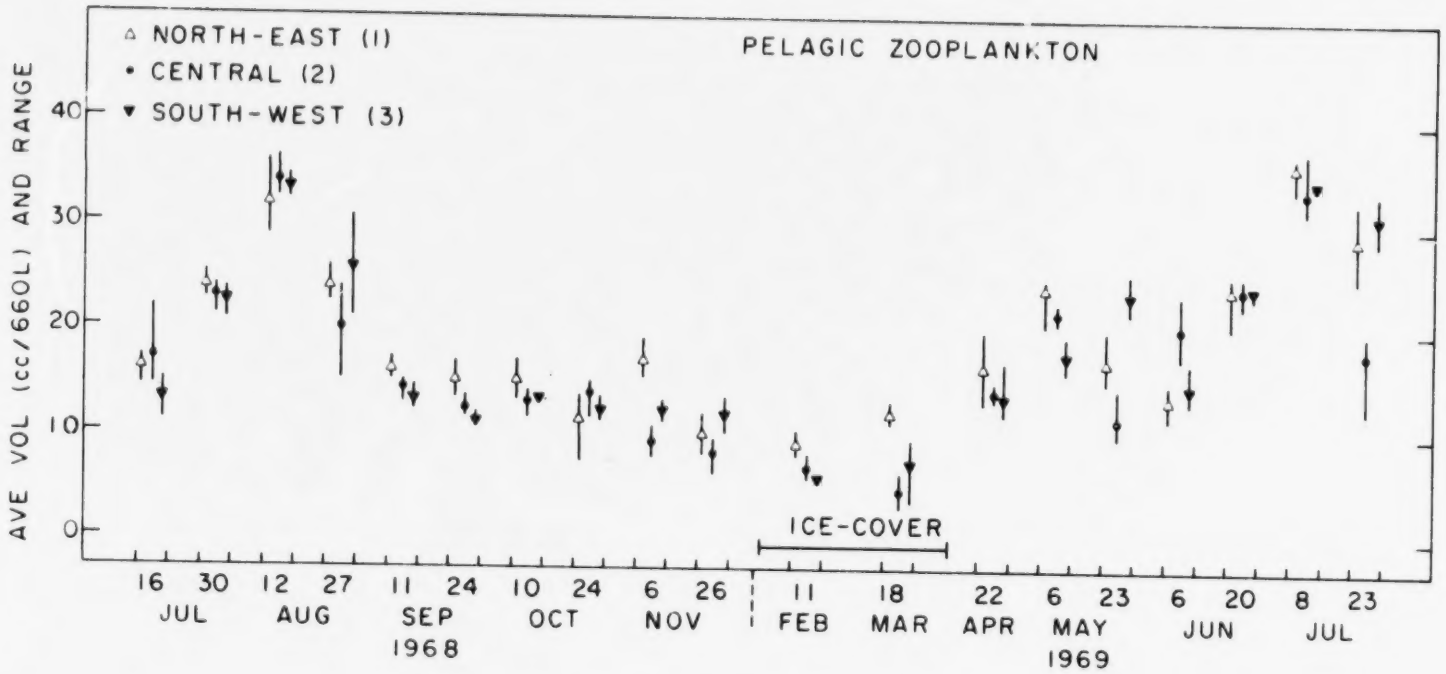

Figure 29. Seasonal changes in the standing crop of pelagic-zooplankton in Lake Wingra.

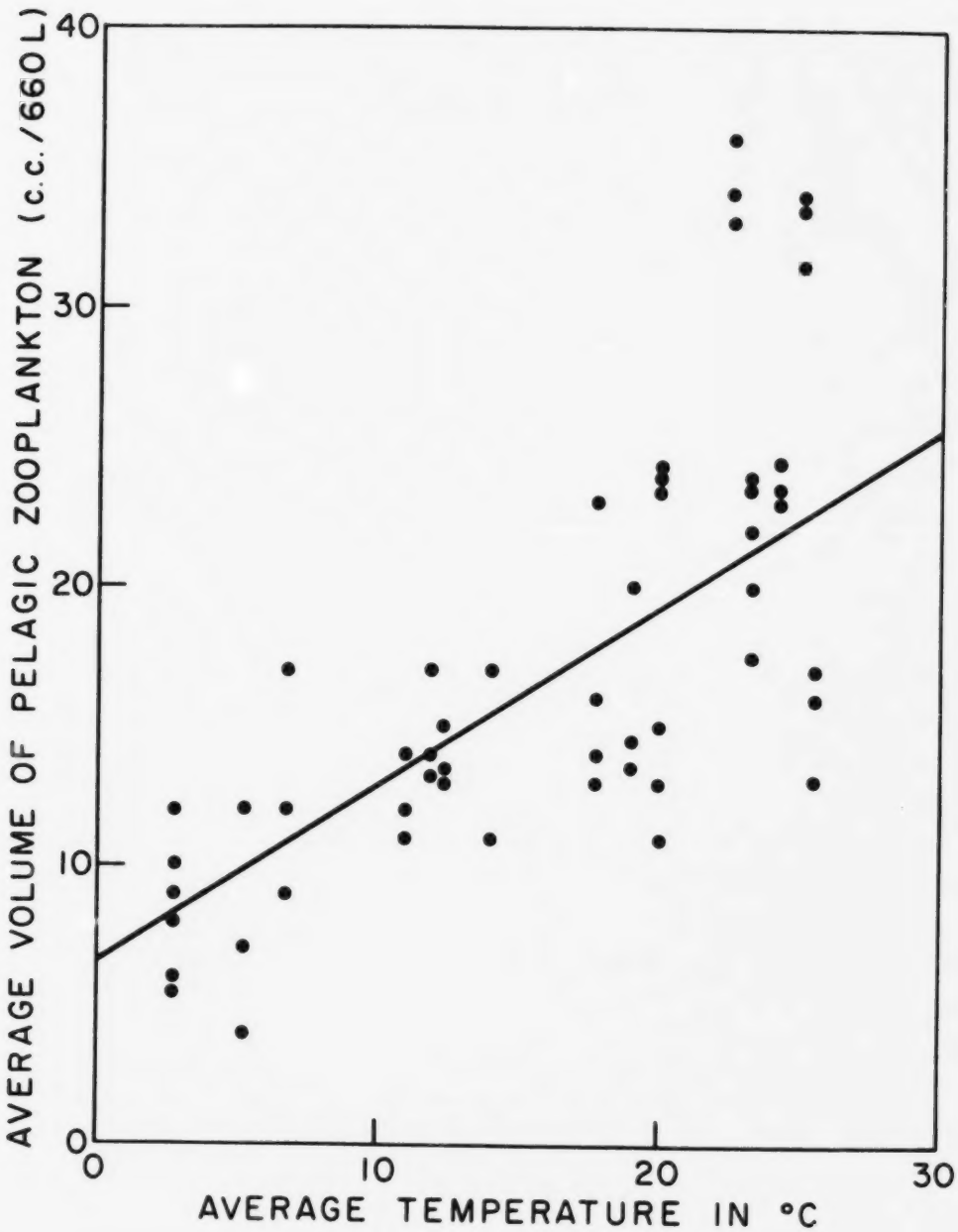

Figure 30. Relationship between standing crop of pelagic-zooplankton and temperature of the lake.

species and does not, therefore, affect greatly the population size of any one species.

Bosmina longirostris, Ceriodaphnia quadrangula, Chydorus sphaericus, Daphnia galeata, Daphnia retrocurva, and Diaphanosoma brachyurum must be seriously considered for future studies, quantifying the role of zooplankton population on the transformation and transportation of energy and nutrients in Lake Wingra. These species are generally most abundant during the summer and autumn when their average densities may be as high as 100,000 per 660 liters (Figs. 16 to 21. Although Bosmina retrocurva and Daphnia galeata are relatively not abundant during the winter, their average densities are still at least 10,000 per 660 liters during this period. Thus, the populations of these two species may have to be studied in the winter as well as in the summer and autumn. Chydorus sphaericus, Daphnia retrocurva, Ceriodaphnia quadrangula, and Diaphanosoma brachyurum need to be studied only during the summer and winter.

The latter six species are known to be herbivores. Furthermore, the adult individuals of these species are of similar small size; thus it would not be unreasonable to assume that the biomass per adult individual of these different species is fairly comparable.

COPEPODS

Cyclops bicuspidatus thomasi, Diaptomus siciloides, and Mesocyclops edax must be considered in the future studies. Cyclops bicuspidatus thomasi and Diaptomus siciloides must be considered throughout the year. However, of these two species, Diaptomus siciloides is more abundant than cyclops in summer and autumn and less abundant than this species in the winter and early spring. Mesocyclops edax occurs in fairly high densities generally only during the summer and is absent during the autumn, winter, and spring.

The feeding habit of only one of these species is known with any certainty. Cyclops bicuspidatus thomasi is primarily a predator.

ROTIFERS

On the basis of data obtained in 1968 and 1969, it does not seem worthwhile to consider the rotifer populations in future studies (quantifying the role of pelagic-zooplankton population of the transformation and transportation of energy and chemicals in Lake Wingra). Species such as Keratella quadrata, Monostyla quadridentata, Notholca acuminata, Synchaeta cblonga, and Voronkowia mirabilis occurred in very low numbers (less than 2 per 2 liters) once or twice during our sampling schedule. Others such as Asplanchna priodonta, Brachionus calyciflorus, Polyarthra eurypterus, and Polyarthra vulgaris occurred for only short periods and never exceeded 30 individuals per 2

per 2 liters (Figs. 26 and 28). Brachionus angularis, Keratella cochlearis, and Tetramastix opoliensis occurred at densities exceeding 30 individuals per 2 liters only on a couple of occasions of very short duration (Figs. 26, 27, and 28). Generally, the density values for the various species were much lower than those recorded in the literature (for example, Hutchinson, 1967).

Most of the species in Lake Wingra (exception is Asplanchna priodonta) are known to feed on algae and bacteria (Hutchinson, 1967). Asplanchna feeds to some degree on other rotifers and small crustaceans. Thus, this species may have to be considered in the studies dealing with population dynamics of certain cladoceran and copepod species.

Seasonal Change in Standing Crop of Pelagic Zooplankton

The seasonal trend in the standing crop of pelagic zooplankton reflects generally the seasonal trends in the abundance (individuals per 660 liters) of most of cladoceran and copepod species (see Figs. 15 to 25 and Fig. 29). Thus, the volume of pelagic zooplankton was greatest during the summer, intermediate during the autumn and spring, and least during the winter. This seasonal trend may be a result of a lack of thermal stratification-cycle in Lake Wingra, absence of heavy predation on the zooplankton during the summer, and no food limitation during the summer.

In lake with thermal stratification-cycle, the typical seasonal trend in the abundance of Daphnia consists of maximum density during late spring and early autumn and low density during the summer (Hall, 1964; McNaught, 1964). This type of seasonal trend is thought to be a result of optimal food availability during late spring and early autumn (when nutrient conditions are ideal for algal growth) and of heavy predation of zooplankton (Hall, 1964; Wright, 1965) or limited food during the summer.

There is a reasonable correlation between volume of pelagic zooplankton and temperature (Fig. 3). Thus, temperature may be used to predict the biomass of pelagic zooplankton in Lake Wingra. This correlation is what one might expect if other conditions (seasonal thermal stratification cycle in the lake, heavy predation on zooplankton during the summer, no food limitation during the summer) did not prevail.

Density and Standing Crop of Zooplankton at the Three Stations

On most of the sampling dates, the variation in the density and standing crops (of most of the species) between the three stations did not seem large (Figs. 15 to 30). This means that it is not necessary to sample more than one small area of the lake (its location is not critical)

to get density values from which population estimates of the species in the lake. Of course, since we are interested in population estimates of the pelagic-zooplankton species, it may be necessary to determine the extent to which these species are distributed shore-ward. This determination would improve the population estimates as volume of water occupied by these species will be better known.

SECTION VI

SEASONAL CHANGE IN THE ABUNDANCE OF OLIGOCHAETES AND CHIRONOMIDS IN LAKE WINGRA

Introduction

The benthos constitutes an important component of a lake ecosystem. Larger insect larvae, for example, may serve as a major fish food organism. The benthic organisms thus serve as a key link to convert detrital sediment material to harvestable food biomass. In this paper, seasonal changes in the abundance of various species of oligochaetes and chironomids during the period from 6 July 1968 to 25 July 1969 are described.

Methods

Five sampling stations were established on Lake Wingra (Fig. 31). Stations 1, 2, and 3 were located on the northeast, central, and southwest portions of the lake, respectively. Station 4 was situated between Station 2 and the south shore, whereas Station 5 was located between Station 2 and the north shore. All five stations had depths of about 3 m. The characteristics of the bottom sediments at Stations 1, 2, 3, and 5 appeared to be very similar. Only at Station 5 did we find marl in the bottom samples.

Two samples were collected from each station at about two-week intervals during the ice-free period, about a six-week interval during the early period of ice cover, and about four-week intervals during the latter part of the ice-cover period. A standard Ekman dredge (15.2 x 15.2 cm) was used to collect the samples, while a bucket with the bottom made of fine wire gauze (mesh diameter of 0.22 mm) was used to concentrate the bottom samples. Wide-mouth bottles (32 oz.) were used for temporary storage of the concentrated samples.

On each sampling date of the ice-free period, we followed the same procedural sequence for obtaining the bottom organisms. The boat was first anchored at the station. This was followed by lowering the opened dredge gently into the bottom sediment. After the sampler was closed, it was hauled rapidly to the surface and placed in the sieving bucket. The sampler was opened inside the bucket to release the bulk of the sediment contained in the sampler. We then lowered the bucket into the lake to allow water to enter it through the gauze bottom. This

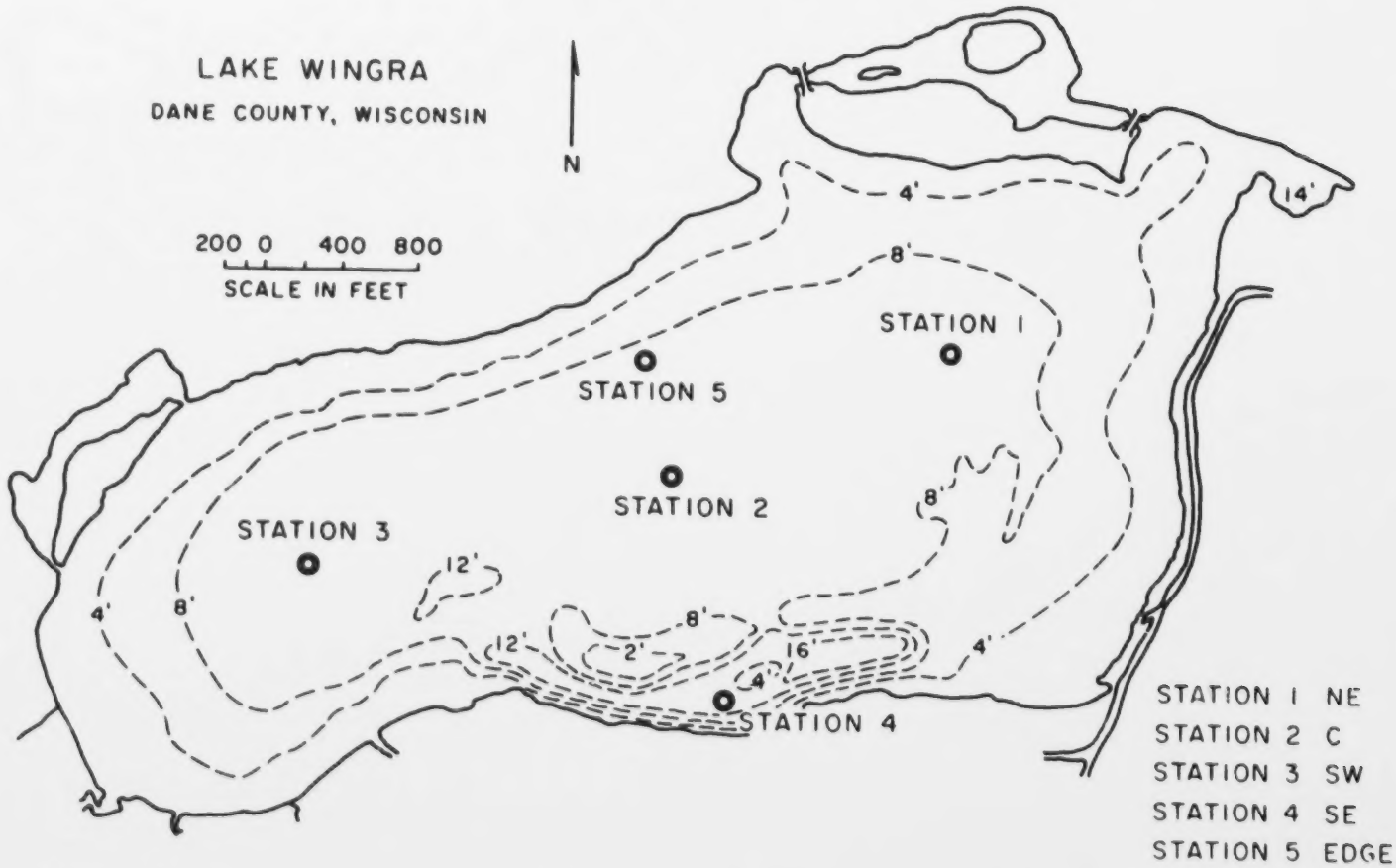

Figure 31. Contour map of Lake Wingra and locations of the sampling stations.

water was used to remove the sediment stuck to the inside of the dredge. The bottom sediment in the bucket was agitated, sifted, and washed to remove most of the sediment and debris. We then washed the remaining content into the bottle.

A slightly different procedural sequence was followed to obtain bottom organisms on sampling dates of the ice-cover period. We made a large opening (2 x 2 m) in the ice at each station. The dredge was handled in the manner described previously. After hauling the closed dredge to the surface, we immediately released the bulk of the bottom sediment into a large plastic bag. With the opened dredge still positioned over the opening of the bag, the sediment still left in the dredge was washed into the bag. The bags containing the samples were taken to the laboratory. All the sediment in each bag was put into the sieving bucket and was subjected to agitation, sifting, and washing. The content remaining in the bucket was washed into the bottle.

A chemical preservative was not added to the bottles containing these reduced samples. Preliminary analysis revealed that live organisms, because of their movement and usually contrasting coloration, could be detected more readily from the debris and sediment present even in these reduced samples. These samples were therefore refrigerated at 2 to 4°C prior to being analyzed for bottom organisms.

Collecting the organisms from each of these reduced samples involved a repetition of the following set of procedures. The content (sediment, debris, organisms, and some water) of the bottle was agitated by a strong stream of water released from a tap. A portion of this content was poured into a steel tray coated with porcelain, and some water was subsequently added to the tray. The organisms in the tray were removed with the use of a fine pair of forceps and a small suction pipette, and were then put into 75% alcohol solution contained in a small vial. When all the organisms were removed, the sediment and debris left in the tray were discarded. These procedures were repeated in the same sequence until the entire sample was analyzed for the organisms.

The chironomids and oligochaetes were identified to species whenever possible. Identification of the genus and/or species of chironomids was based on the labial appendages of type specimens prepared by Dr. William Hilsenhoff, Department of Entomology, University of Wisconsin. To identify the chironomids in our samples, we mounted their heads on slides and examined the labial appendage with a dissecting scope (Bausch and Lomb) set at a magnification of 120X. Identification of the species of oligochaetes was based on the keys developed by Brinkhurst (1964 and 1965) and on type specimens prepared by us with the assistance of Dr. Ralph Brinkhurst, Department of Zoology, University of Toronto. Relatively few chironomids and oligochaetes could not be identified confidently to species.

In the presentation of our results, the density of various species of oligochaete and chironomids is expressed as number per 8 samples, or as average number per 2 samples (plus or minus one residual). The first expression of density (after sorting) was used to examine the change in the abundance of oligochaetes and chironomids at the various sampling stations during the study period. The second expression, $\bar{x} \pm \frac{1}{n}\sum_{i=1}^{n} |r_i|$, (where $\bar{x}$ = mean; n = sample size; and $|r_i| = x - \bar{x}$ = absolute value of the i^{th} residual) was used to obtain representative density values for different stations for the four seasonal periods of the year.

Some physical and chemical variables were monitored at Station 1 during this study. Temperature, light penetration, and oxygen concentration were measured with a thermometer, secchi disc, and modified Winkler Method, respectively. Conductivity was measured at approximately 2 to 4 week intervals, whereas oxygen was monitored at 1 to 2 week intervals. To obtained temperature data for every sampling day and light penetration data for every sampling day of only the sensitive months, oxygen profile was determined at 4-6 week intervals. These data are presented in Fig. 2.

Results

Oligochaeta

Five species of oligochaetes were found to be common in grabs collected during our study period. These were Limnodrilus hoffmeisteri (Tubificidae), Limnodrilus udekemianus (Tubificidae), Tubifex tubifex (Tubificidae), Tubifex ignotus (Tubificidae), and Lumbriculus variegatus (Lumbriculidae). Of the five oligochaete species collected, only T. tubifex and L. variegatus occur cumulated growths at Hamilton Harbour and T. ignotus. Since the latter is found in the organic sediments of the Harbour, it may also be Limnodrilus hoffmeisteri. Limnodrilus udekemianus, Tubifex tubifex, Nais communis, and Nais variabilis were also found in the Harbour, but only in low densities. Only two (3.7%) of the specimens were Stylaria lacustris. Stylaria lacustris was indeed rare as only 1 (0.3%) individuals of this species were encountered during the study. Immature oligochaetes could not be identified to genera or species (Table 1).

Limnodrilus hoffmeisteri - cumulation

Seasonal pattern in the abundance of three Tubificids (mainly L. hoffmeisteri) was not consistent between stations (Fig. 3a). The density of these oligochaetes at Station 1 (Randle's) did not change

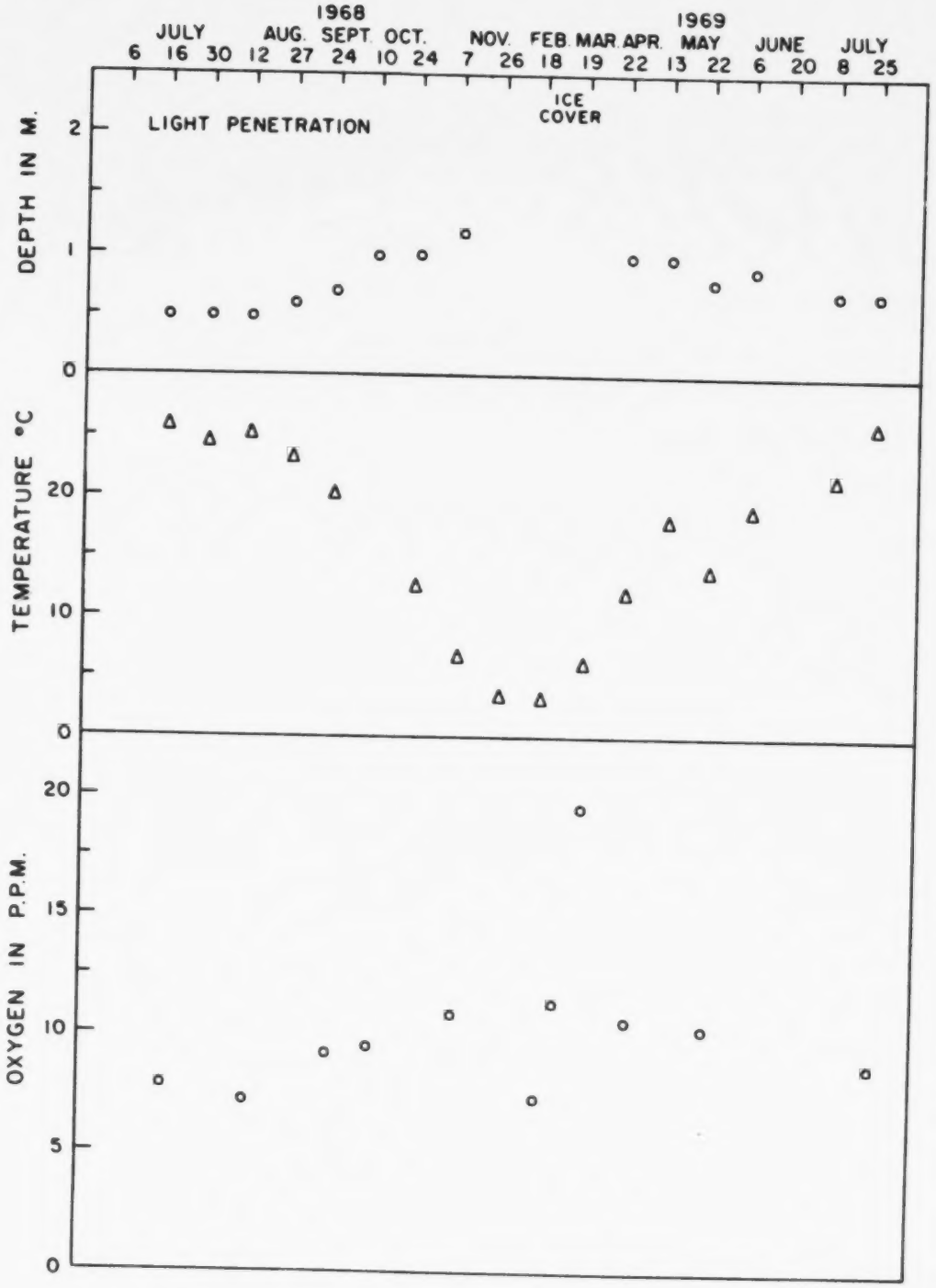

Figure 32. Light penetration, average temperature and average oxygen concentration at Station 2 (c) in Lake Wingra.

Table 3. Species and abundance of cligochaetes and chironomids in the sediment of the open-water region of Lake Wingra. From July 1968 to August 1969.

Oligochaetes	Total Number	Percent of Total
Limnodrilus hoffmeisteri and *L. udekemianus* combined	1069	49.9
Euilydrilus hammoiensis	924	43.2
Ilyodrilus templitoni	122	5.7
Stylaria lacustris	7	0.3
Unknowns	19	0.9
	2141	100

Chironomids	Total Number	Percent of Total
Chironomus plumosus	1091	76.9
Chironomus attenuatus	45	3.3
Procladius sp.	104	7.4
Tanypus sp.	170	11.9
Unknowns	7	0.5
	1417	100

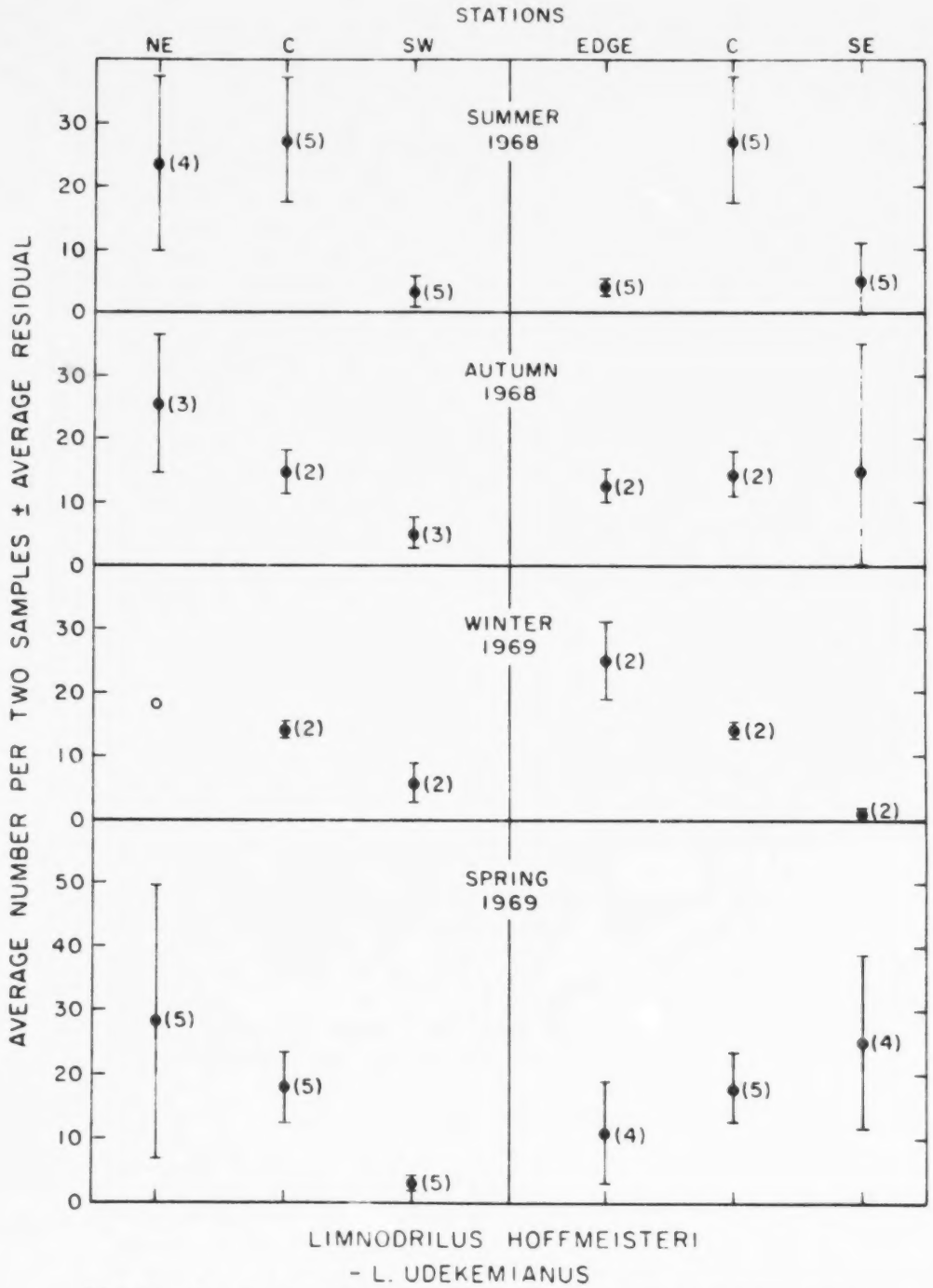

Figure 33. Seasonal changes in the abundance of Limnodrilus hoffmeisteri (includes L. udekemianus). Solid bar indicates abundance based on 2 samples, whereas clear bar represents abundance based on 1 sample. L indicates no data as a result of samples drying during storage, while 0 represents zero abundance on the basis of one sample.

significantly during the year; it rarely exceeded 5 per two samples. Although the density ranged from about 5 to 39 per two samples at Station 3 (central), a seasonal pattern in abundance was not clearly evident. With the exception of four sampling dates (6 July 1968, 12 August 1968, 13 May 1969), the density never exceeded 20 per two samples at this centrally located station. At Station 1 (northeast), the number of individuals per two samples ranged from about 1 to 77, but the seasonal trend in abundance was not clear except for a sharp increase and subsequent rapid decrease in abundance during the spring of 1969. The change in abundance of these oligochaetes at Station 4 (northeast) during spring of 1969 was similar to that at Station 1. Unique to Station 4 was, however, the lack of individuals on many of the sampling dates. There appeared to be a distinct seasonal trend in abundance at Station 5 (edgewood); density increased gradually from about 5 per two samples to about 30 per two samples during the period from 6 July 1968 to 18 February 1969, and it decreased quite sharply to about 1 per two samples from 18 February to 25 July 1969.

Euilydrilus hammoiensis

Seasonal trend in the abundance of this species was fairly consistent between stations (Fig. 34). Although the density at Station 3 remained within a narrow range of 0-6 per two samples, there appeared to be a seasonal trend consisting of a progressive increase in density to maximum from winter to late spring, progressive decrease in abundance from late spring to the end of autumn. Seasonal trends in abundance at Stations 2, 1, and 4 were reasonably similar and consisted of relatively low density during the summer, autumn and winter, abrupt increase in density to maximum during early spring, and fairly pronounced decrease in abundance during late spring. The initiation of the abrupt increase in density observed at these 3 stations seemed to coincide with the time at which the lake became open. Seasonal pattern in abundance at Station 5 differed slightly from those at Stations 2, 1, and 4; no organisms were present on many of the sampling dates of summer and early autumn, and there was a pronounced increase in density in late autumn.

Ilyodrilus templitoni and Stylaria lacustris

These two species did not occur in adequate numbers to describe reliably their seasonal trend in abundance. Of 122 specimens of Ilyodrilus templitoni which were collected during our study, 50% of them were recorded on one sampling date (6 July 1968). Only seven individuals of Stylaria lacustris were found during our investigation, and all of them occurred on one sampling date (6 July 1968) at Station 2.

CHIRONOMIDS

Only three genera of chironomids were present in the bottom sediments

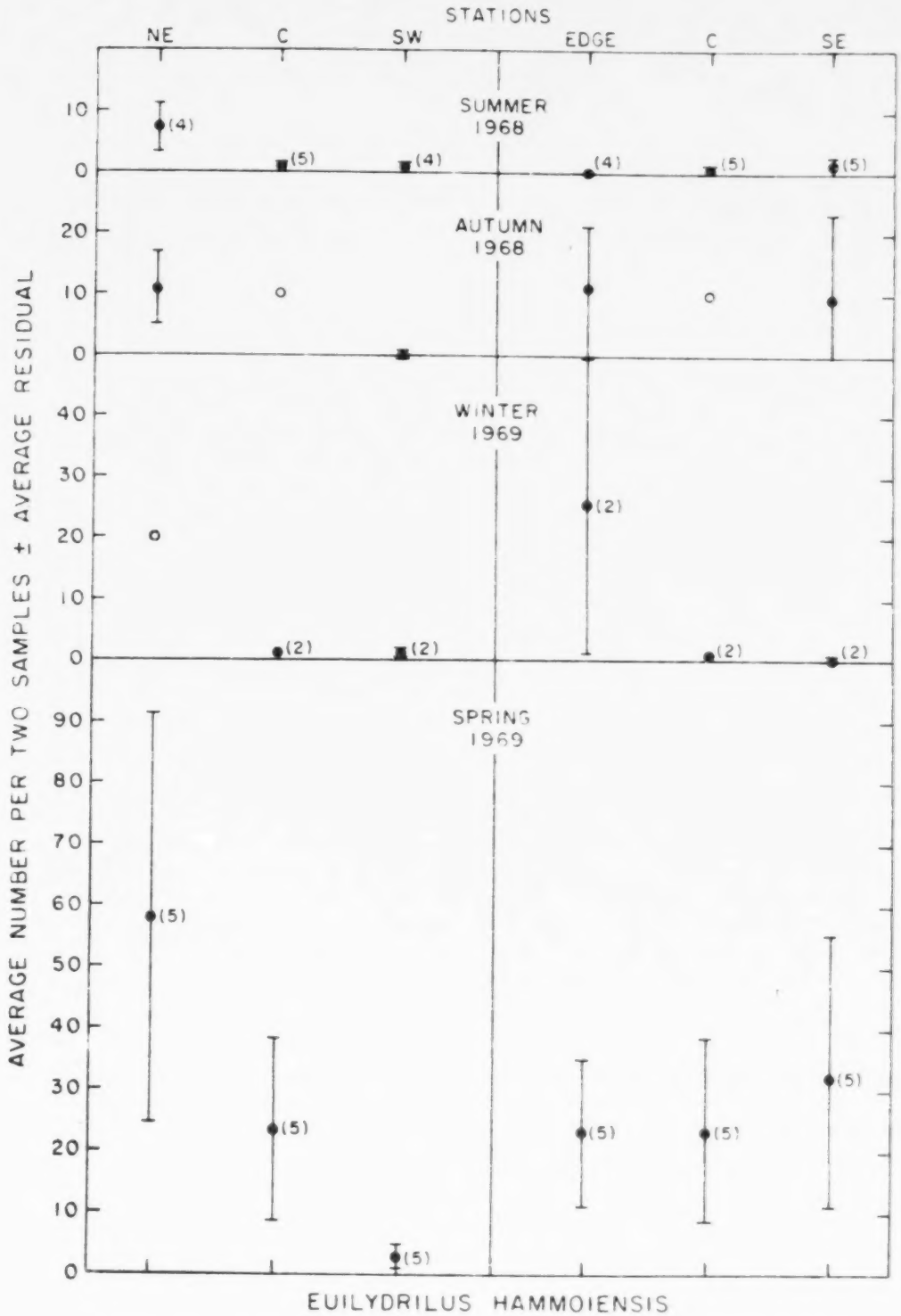

Figure 34. Seasonal changes in the abundance of Euilydrilus hammoiensis at the five sampling stations.

of the open-water region of Lake Wingra. These were Chironomus, Procladius, and Tanypus. The species of Chironomus were C. plumosus and C. attenuatus, but the species of the other two genera were not known. Of 1417 chironomids collected during the study, 1091 (76.9%), 45 (3.3%), 104 (7.4%), 170 (11.9%), and 7 (0.5%) were C. plumosus, C. attenuatus, Procladius sp., Tanypus sp., and unknowns, respectively.

Chironomus plumosus

Seasonal trend in the abundance of this species was fairly consistent between stations (Fig. 35). The density rarely exceeded 10 per two samples at all stations during the summer of 1968. An abrupt increase in numbers was observed in early autumn at most of the stations, and relatively high density ranging from 20 to about 40 per two samples was maintained during early autumn and winter. A sharp decrease in numbers shortly prior to or shortly after the end of the ice-cover period was obvious at all stations. This sharp decrease in density was generally followed by further decrease in abundance until an obvious minimum density of less than 4 per two samples was reached. At all stations, there was an abrupt increase in density between 6 and 20 June 1969.

Procladius sp.

Although the density of this species was less than 10 per two samples throughout the study, there was a noticeable seasonal pattern in abundance which appeared similar at all stations (Fig. 36). Few individuals of Procladius were present on at least half of the sampling dates during the summer of 1968. In contrast, no individuals were present on most of the sampling dates during the autumn and winter. Typifying the sampling dates of the spring and summer of 1969 was the consistent presence of few to several individuals.

Tanypus sp.

The density of this form never exceeded 10 per two samples during the study period, and the seasonal trend in the abundance of this organism was not noticeably clear (Fig. 36). Only in the spring was the density maintained relatively high at all stations.

GRADIENT IN THE ABUNDANCE OF BENTHIC ORGANISMS

Benthos gradients in Lake Wingra were determined for the four seasons, summer of 1968, autumn of 1968, winter of 1968-1969, and spring of 1969. Data collected from 6 July through 27 August 1968 were "pooled" to obtain average number per two samples and residual at each station for this summer period. Data taken from 24 September through 26 November 1968

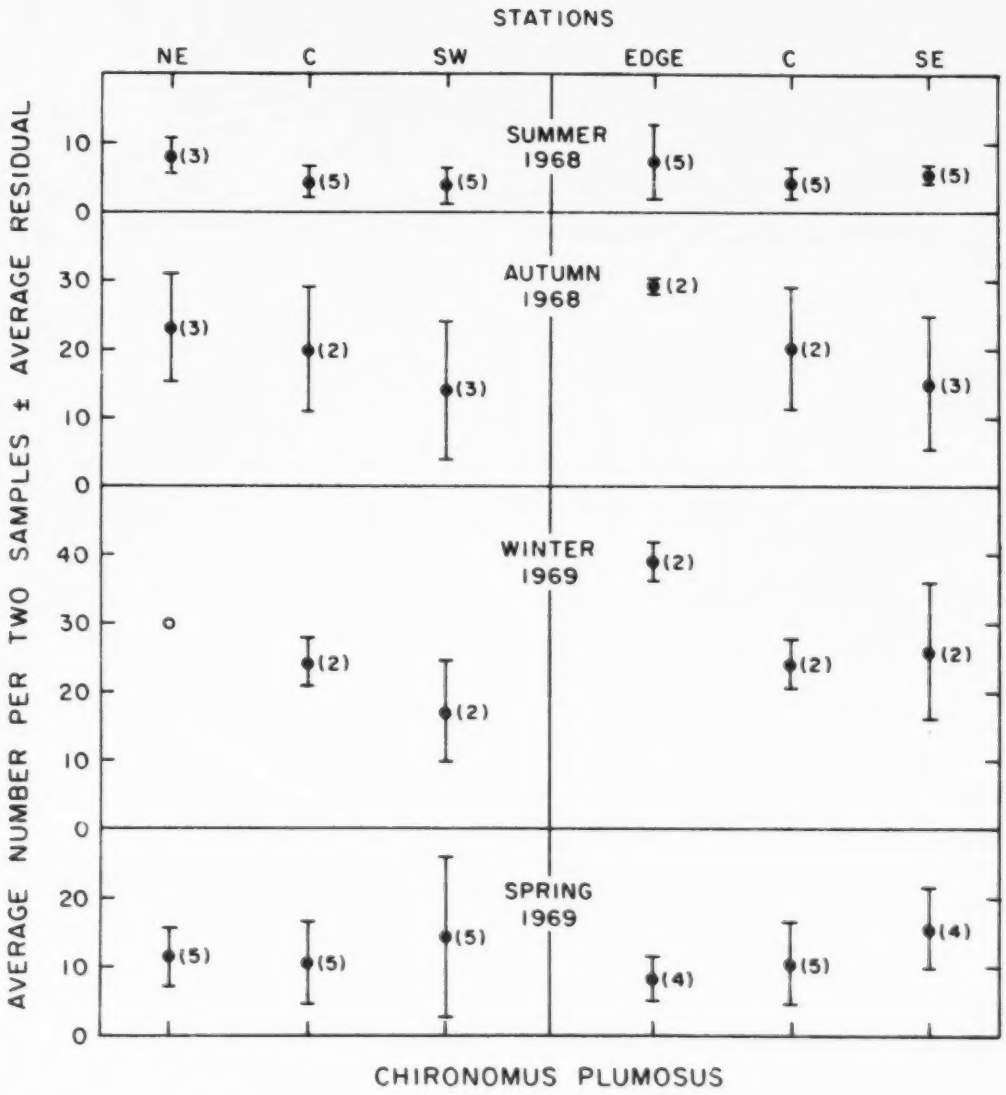

Figure 35. Seasonal changes in the abundance of Chironomus plumosus at the five stations.

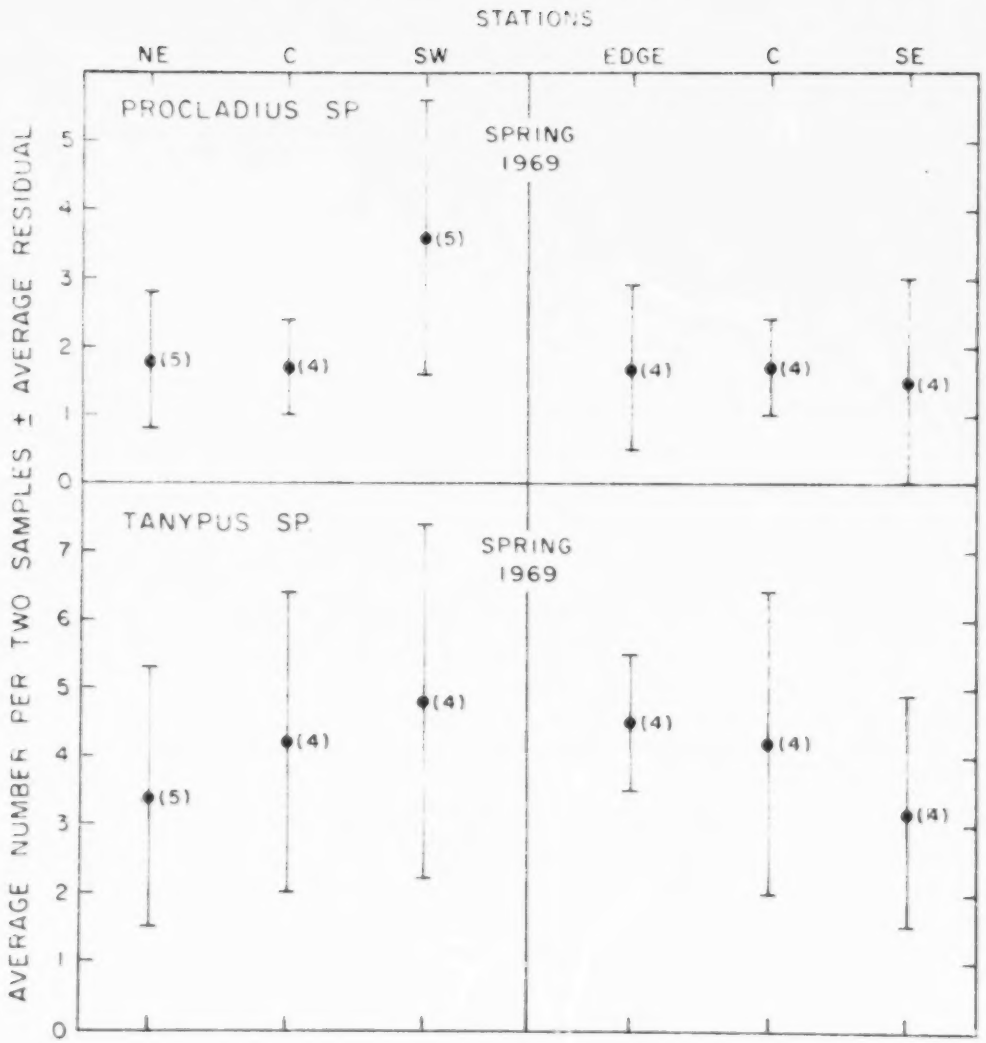

Figure 36. Seasonal changes in the abundance of Procladius sp. and Tanypus sp. at the five sampling stations.

were used to derive average numbers per two samples and residual at each station for the autumn period. Only the density measurements obtained on 18 February and 19 March 1969 were used to calculate average abundance and residual for the winter period. Results obtained on 22 April, 13 May, 22 May, 6 June, and 20 June were used to obtain statistics representative of the spring period. For any seasonal period with two sampling dates having one sample each, the counts were "lumped" and expressed as number per two samples. For any season with three sampling dates having one sample each, two samples were randomly selected from the three and the counts expressed on the basis of these two samples.

No representative statistics were computed for the summer of 1969 because two sets of counts based on two samples were rare due to one of the pair of samples being lost as a result of drying.

OLIGOCHAETES

Limnodrilus hoffmeisteri (+L. udekemianus)

The seasonal average density of these organisms at Stations 3, 2, and 1 were calculated to characterize their density pattern along the long axis of the lake (Fig. 37). Low, intermediate, and high densities were consistently associated with Stations 3, 2, and 1, respectively, during the autumn, winter, and spring. These results suggested a fairly linear increase in average density from Station 3 to Station 1. Density relationship between stations for the summer was an exception as the highest density was at Station 2. Even for the summer, Station 3 had the lowest density.

The average density at Stations 5, 2, and 4 was determined to assess the density pattern along the short axis of the lake (Fig. 38). Density relationship between stations differed with seasons. For the summer, the highest density was at Station 2, and the lowest at Stations 5 and 4 (densities at these two stations were similar). For the autumn, the densities at Stations 5, 2, and 4 were similar.

The density pattern for the winter consisted of the highest value at Station 5, intermediate at Station 2, and lowest at Station 4. For the spring, the density relationship was just the opposite to that of winter, with highest abundance at Station 4 and lowest at Station 5.

Euilydrilus hammoiensis

For the species, the density relationship between stations situated along the long axis of the lake was similar only for summer and winter (Fig. 38). Relatively high density at Station 1 and virtually identical low density (less than 2 per two samples in all cases) at Stations 2 and 3 were characteristic of these two seasons. In contrast, relatively high

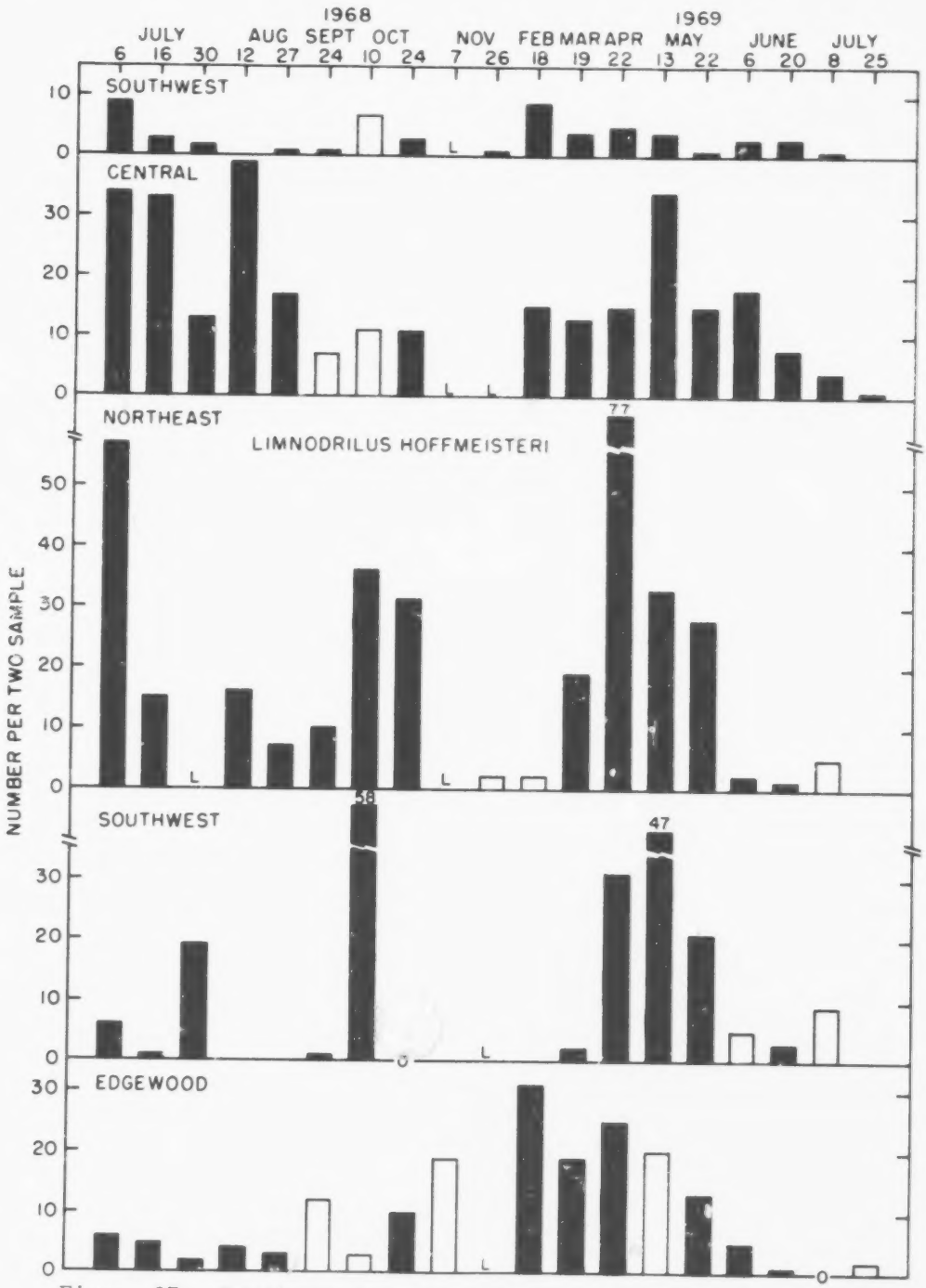

Figure 37. Gradients in the abundance of Limnodrilus hoffmeisteri (includes L. udekemianus) along the long and short axis of Lake Wingra at different seasons. Number enclosed in brackets represent sample size used to calculate the statistics. Open circle does not represent an average as only one pair of samples was available.

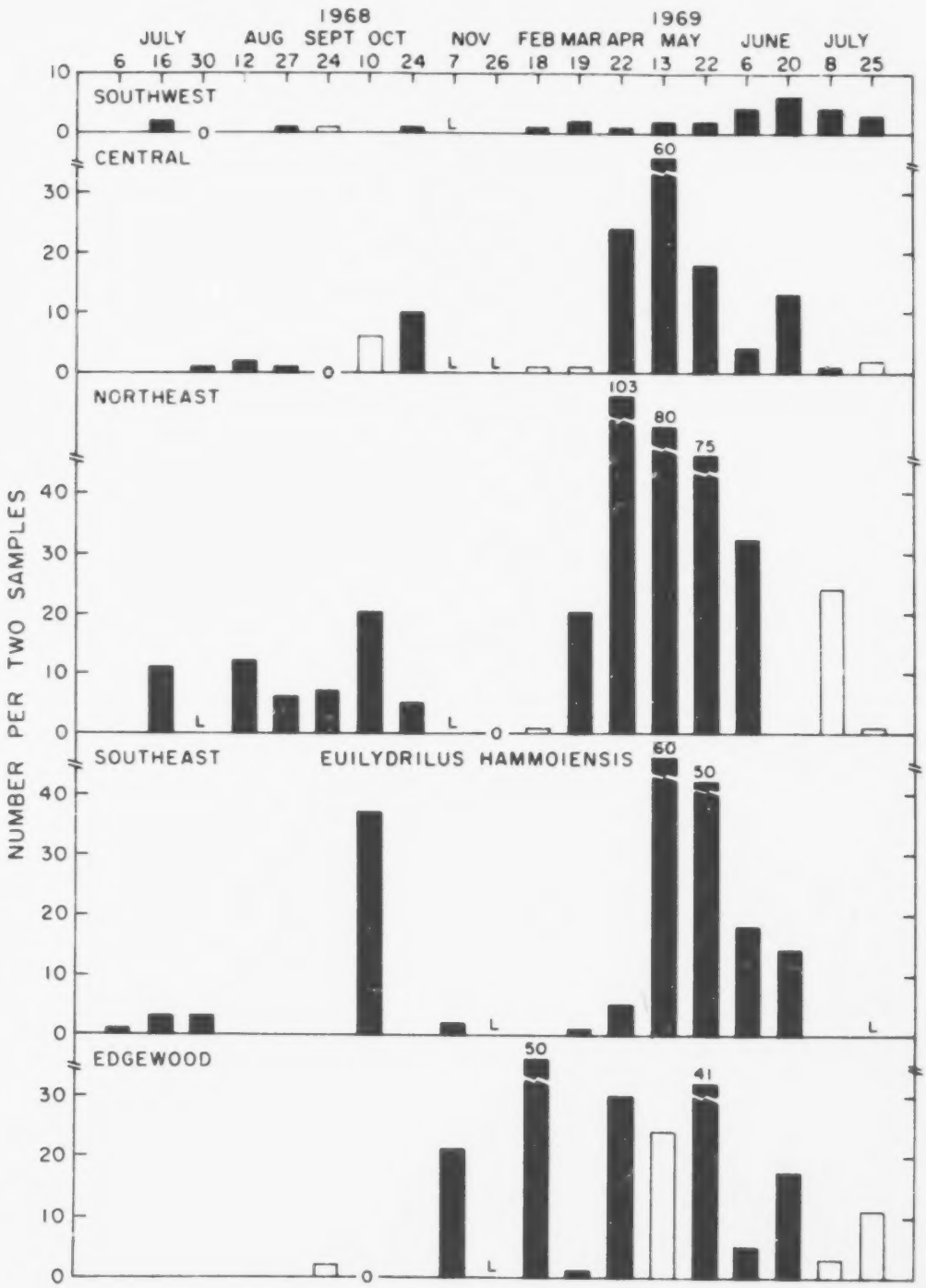

Figure 38. Gradients in the abundance of Euilydrilus hammoiensis along the long and short axis of Lake Wingra at different seasons.

and similar density at Station 2 and 1 and low abundance at the other station were observed for autumn. For the spring, the high density was at Station 1, intermediate at Station 2, and lowest at Station 3.

The density relationship between stations located along the short axis of the lake was similar only for summer and autumn (Fig. 38). Stations 5, 2, and 4 had comparable average density during these seasons; however, the average density values ranged from 0 to about 2 for the summer, and from 9 to 11 for the autumn. Seasonal average density at Stations 2 and 4 was similarly low (less than 2 samples) and that at Station 5 was high (about 26 per two samples) for winter. For spring, the highest average density was at Station 4, and lowest, but identical density (23.7 per two samples) at the other two stations.

CHIRONOMIDS

Chironomus plumosus

Only for autumn and winter was there a similarity in the density relationships between Stations 3, 2, and 1 (Fig. 39). For these seasons, there appeared to be an association of highest density with Station 1, intermediate with Station 2, and lowest with Station 3. For the summer, Station 1 had a comparatively high abundance, and Station 2 and 1 had similar, low density. The density relationship between stations for spring was opposite to that of autumn, with highest average density at Station 3 and comparable values at the other two stations.

Stations 5, 2, and 4 have a similar density relationship for summer and winter and an opposing relationship between autumn and spring (Fig. 40). For the former two seasons, Stations 2 and 4 had a comparable average density which was less than that of Station 5. The difference between the density at Station 5 and that at the other two stations was small for the summer and large for the winter. Highest, intermediate, and lowest densities were associated with Stations 5, 2, and 4, respectively. in the autumn and with Stations 4, 2, and 5, respectively, in the spring.

Procladius sp.

Only for the spring were there adequate data to compute average density of this organism at Stations 1, 2, 3, 4, and 5 (Fig. 40). Density relationship between stations established along the long axis of the lake consisted of a relatively high abundance at Station 3, and low, but similar, density at Stations 2 and 1. Average density at Stations 5, 2, and 4, situated along the short axis, was, however, similar for the same seasonal period.

Tanypus sp.

Adequate amount of data was also restricted to the spring for this

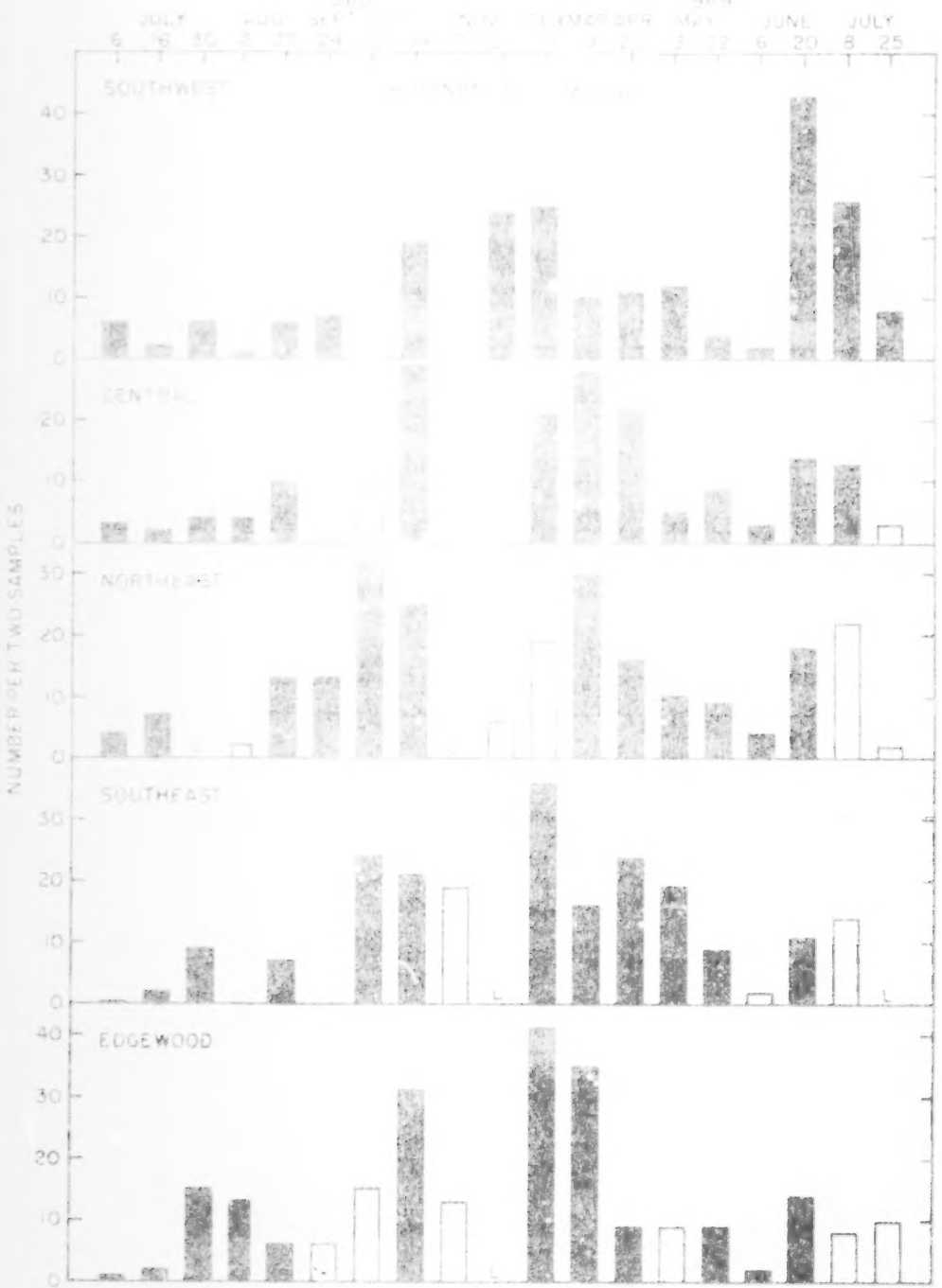

Figure 29. Gradients in the abundance of Chironomous plumosus along the long and short axis of Lake Wingra at different seasons.

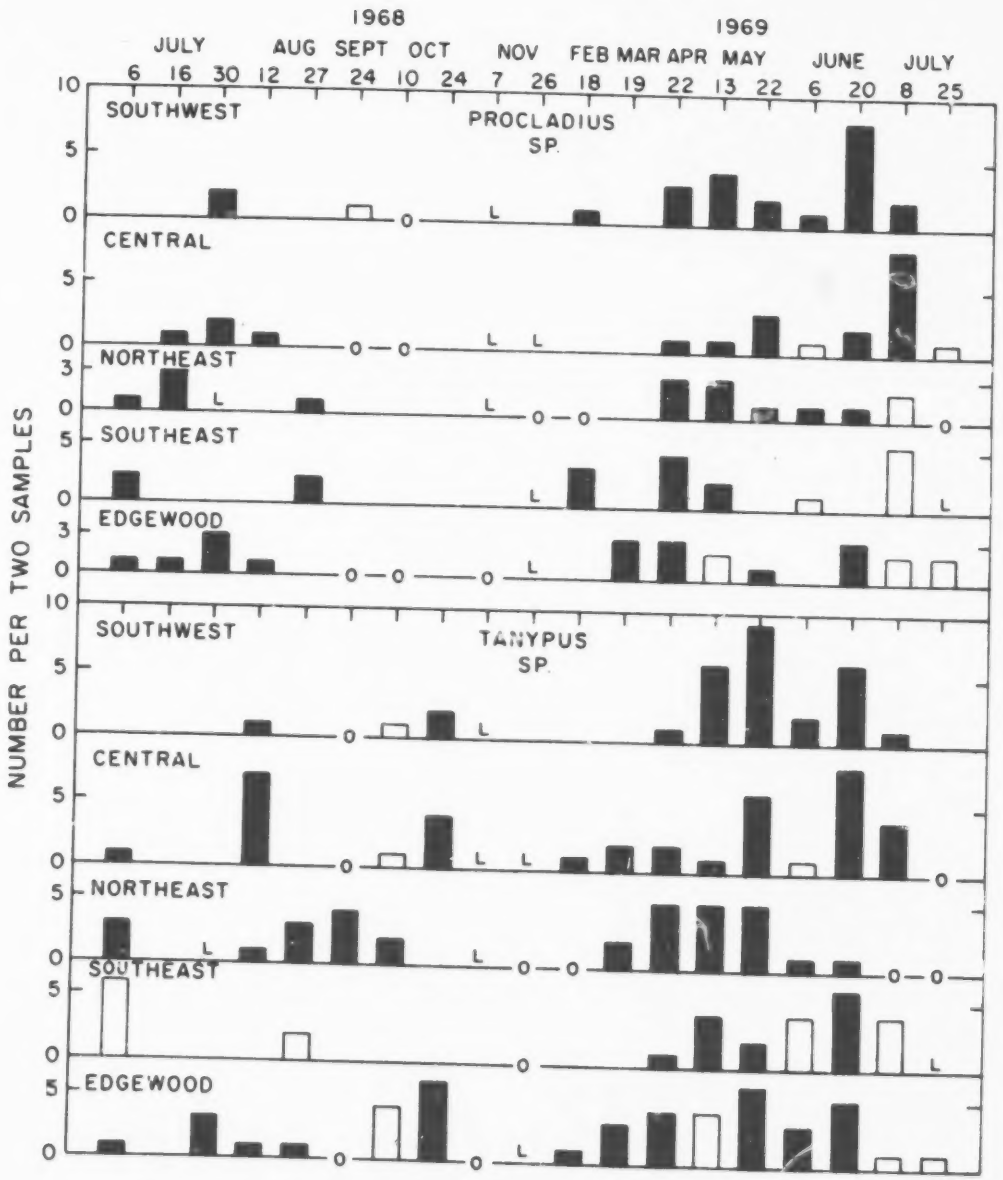

Figure 40. Gradients in the abundance of Procladius sp. and Tanypus sp. along the long and short axis of Lake Wingra. Spring, 1969.

organism (Fig. 40). Highest, intermediate, and lowest densities were at Stations 3, 2, and 1, respectively. For stations situated along the short axis, highest, intermediate, and lowest abundance were associated with Stations 5, 2, and 4, respectively.

Discussion

The predominant benthos of Lake Wingra are Limnodrilus hoffmeisteri, Euilydrilus hammoiensis, and Chironomus plumosus. These species are almost equally abundant as 1069 L. hoffmeisteri, 924 L. hammoiensis, and 1091 C. plumosus were collected during our sampling period from early July 1968 to mid-July 1969.

Limnodrilus hoffmeisteri

Seasonal trend in the abundance of L. hoffmeisteri is neither distinct at all stations nor consistent between stations (Fig. 33). Lack of discrete seasonal pattern in abundance may be due in part to the lack or incompleteness of data on some of the sampling dates as a result of losing samples through drying. However, since data are absent or incomplete on many occasions for comparable dates for the different stations, the consistency in the seasonal trend between stations should not be affected by this aspect. There is, nevertheless, a lack of similarity in the seasonal pattern at the different stations (Fig. 33): this suggests the existence of local variations in the seasonal trend of environmental factors influencing this species.

The highest density of L. hoffmeisteri which has been encountered during the study is 77 per two samples. This is roughly equivalent to 1617 per square meter, a density far less than most recorded by Hiltunen (1969) for the western basin of Lake Erie, by Brinkhurst (1967) for Saginaw Bay, and by Brinkhurst (1970) for Toronto Harbour, Lake Ontario. In spite of this comparatively low abundance of this oligochaete in Lake Wingra, there are distinct gradations in its density along both the long and short axis of the lake.

The most consistent density gradient for the long axis is a fairly linear increase in density from Station 3 to Station 1, or from the southwest portion to the northeast portion of the lake (Figs. 38 and 31). Similar results have been found by Brinkhurst (1967) at the mouth of the Saginaw River, and by Hiltunen (1969) at the mouth of the Detroit and Maumee Rivers. Both investigators have observed a decreasing density with increasing distance from the mouth of the rivers. The trend in density along the long axis of Lake Wingra is opposite to those observed by Brinkhurst and by Hiltunen; the lowest density is at the inlet side of the lake, and the highest at the outlet side of the lake. These results suggest

that the bottom sediment of Lake Wingra may have increasing amounts of organic material from the southwest to the northeast side of the lake, and that the inlet (or inlets) at the southwest side is not the major source of organic material entering this lake.

Density relationship between stations located along the short axis of Lake Wingra is not as seasonally consistent as that between stations situated along the long axis (Figs. 37 and 31). It is different for every season (Fig. 37). We do not have any plausible explanation for this seasonal variation in density relationship.

Euilydrilus hammoiensis

Seasonal trend in the abundance of Euilydrilus hammoiensis is fairly distinct at all stations and also consistent between stations (Fig. 34). For all stations, low abundance is associated most frequently with summer, autumn, and winter, whereas high density is associated most often with spring. These results suggest that this species has one generation per year in Lake Wingra.

Density relationship between stations along the long axis of the lake indicates not only a striking difference in density between the three stations (3, 2, and 1), but also an increasing density of this organism with increasing distance from the southwest portion of the lake (Figs. 39 and 31). This density gradient is fairly similar for different seasons, but is not as linear as that observed for L. hoffmeisteri. The availability of more organic material with increasing distance from the southwest portion of the lake is also suggested from this trend of E. hammoiensis.

Densities of E. hammoiensis at the three stations positioned along the short axis of the lake are not similar in all seasons (Figs. 38 and 31). Only in spring and summer are there comparable density at the three stations. The reasons for seasonal change in the density relationship between the three stations are not known.

Chironomus plumosus

Seasonal pattern in the abundance of this species is not only fairly distinct, but also remarkably consistent between stations (Fig. 35). The decline in the abundance of this organism during the spring for all stations probably reflects the loss of larvae (fourth-instar) from the lake through emergence. Abrupt increase in larval density from 6 June to 20 June 1969 may reflect the hatching of another generation of larvae.

Density relationship between stations along the long axis of the lake indicates only a slight difference in density between the stations for most of the seasons (Figs. 39 and 31). There is generally only a slight

linear increase in density with increasing distance from the southwest portion of the lake, and this density gradient is less pronounced than those for the two oligochaete species. This gradient for C. plumosus may also reflect a gradient in the amount of organic material available to them along the long axis of the lake.

Density relationship between stations along the short axis of the lake is fairly consistent as there is a general tendency for density to increase from Station 4 (southeast side of the lake) to Station 5 (edgewood or northwest side of the lake) (Figs. 39 and 31). The only exception to this trend is in the spring. A fairly consistent density relationship between stations along this axis for this species and not for the two major oligochaete species suggests that the amount of organic material is not necessarily the common factor per the abundance of the three species.

General Remarks

From the standpoint of numbers, Limnodrilus hoffmeisteri, Euilydrilus hammoiensis, and Chironomus plumosus are most prominent. However, numerical prominence does not necessarily mean that these benthic organisms are the most important of the benthos in terms of their contribution to energetics and nutrient cycling in Lake Wingra. Until acceptable data on the turnover rates of these organisms are available, the true importance of these species cannot be assessed. Especially important for the determination of turnover rates are the rates at which these benthic organisms are being eaten by the fishes in this lake. Studies on food preference and feeding rates of the fishes have not been completed yet. Until such studies are completed, whether numerical prominence reflects true importance of these species with respect to energetics and nutrient cycling cannot be determined.

The role of benthic organisms in the transport and transformation of energy and nutrient through lakes can best be studied with the consideration of population dynamics. To investigate the population dynamics of these organisms, one can measure the total population or concentration of individuals. Since population attributes based on total population are logistically impossible to measure, one is usually forced to deal with concentration or density for these purposes. It is usually assumed that the density monitored is quite representative. However, for benthic organisms in Lake Wingra, the attainment of representative density is still a very difficult problem. Knowing that the seasonal trend and density of the organisms varies with location, one must establish one to several stations from which he can collect representative samples. The establishment of these strategic stations

will be difficult as they must reflect representative seasonal trend as well as representative density. Thus, even to treat the dynamics of these organisms on a density basis is a monumental task. If the stations are not carefully selected, the results from the study will have no meaning to Lake Wingra, the energetic and nutrient dynamics of which one wishes to describe.

SECTION VII

DIEL PATTERNS OF DISTRIBUTION AND FEEDING OF SELECTED FISH SPECIES IN LAKE WINGRA

Introduction

An important objective of this study is understanding the community structure and energy dynamics of fish populations in the lake. A previous thesis completed on the ecology of the panfish in the lake (Helm, 1958) raised questions and indicated areas in which greater study was needed. Helm's data supported a theory of spatial segregation of potentially competitive species. Also present in Helm's work was evidence for diel migrations by certain species.

With the research reported, we have tried to clarify these points. Four species most abundant in open water were chosen for study: bluegill (Lepomis macrochirus), pumpkinseed (Lepomis gibbosus), white crappie (Pomoxis annularis), and yellow bass (Morone mississippiensis). Bluegill were sufficiently numerous that separate limnetic and littoral feeding habits could be studied as well as competition among size classes. Food resources of the various species were studied along with predator prey relations. Revealing energy flow patterns and interaction among the dominant panfish species was the main goal of the investigation.

Sampling Techniques

Fish were sampled by trawling in the limnetic zone and by electric shocking in the littoral zone. The otter trawl, a shrimp try net, measured five meters across and had a maximum vertical gape of approximately one meter during the tows. In the open water series, a complete circuit of the lake was made with the trawl. This series consisted of samples every four hours over a 48-hour period once every month from April through November, 1970. On September 17-18, 1970, additional tows were run in straight lines down the long axis of the lake. These were taken at three hour intervals over a 24-hour period. All hauls within a series were consistent in speed, length, and location in the lake.

Only in September was shocking in the littoral zone used in conjunction with trawling in open water. A transect was shocked both preceding and following each trawl haul. Transects, one at each end of the lake, extended from open water to the shore (approximately 50 meters). The generator was a three phase AC type rectified for a DC output of approximately sixteen amps. Two sections of pipe suspended under the barge and one meter lengths of spring hung from these by eyebolts formed a

large cathode, which enabled us to maximize the usable current. The anodes were 75 cm circles of 2.5 cm diameter copper tubing. The tubing was attached to an insulated handle containing wires leading to the anode. An individual electrode had an effective range of approximately 1 1/4 meters. The gear was mounted on a 5 1/2-meter pontoon barge powered by a thirty-five horsepower outboard motor. Two electrodes were used on every run. Fish swimming towards the electrodes were dipnetted from the water.

Up to one hundred individuals of each species captured during the open water trawls were measured and any remaining were counted. Total length was measured by punching the length on acetate sheets. These measurements were later grouped at 5mm intervals. All fish were released alive in the center of the lake.

During September all fish taken by both sampling methods were frozen on dry ice in the field. We later measured and counted all fish taken in September and subsampled for stomach analysis. Only pumpkinseed, yellow bass, white crappie, and bluegill (three size classes) were numerous enough to permit analysis of food. Ten fish from each species or size class were dissected for each time period and method of capture. For bluegills ten small (75-95mm), ten medium (105-125mm), and ten large (135mm and above) were analyzed. These three size classes were chosen to include the three maxima in September size frequency distributions. The intervening intervals were omitted to eliminate borderline individuals which might have had intermediate characteristics. The intestine was clamped at the pyloric sphincter and the esophagus was cut at the entrance to the stomach. With a forceps the stomach contents were squeezed into a weighing pan. Contents (wet weights) were weighed to 0.0001g and expressed as a percent of body weight. The mean and standard deviation from the mean were computed for each subsample.

Stomach contents were preserved with a ten percent formaldehyde solution for qualitative analysis. Bluegill (three size classes), pumpkinseed, white crappie, and yellow bass were analyzed qualitatively for the 1600 hour series open water trawls, and the 135mm and above group was also analyzed for the 1600 hour series in the littoral zone. For the most efficient use of the available equipment, stomach contents were combined in five groups of two fish each for analysis. With those stomachs containing few zooplankters, we counted all organisms in the sample. When large numbers of zooplankters occurred, subsamples were taken. Organisms were strained from the sample through plankton netting and then washed into a flask with 100ml of water. The flask was agitated on a Genie Mixer to distribute the zooplankton evenly throughout the solution. A one ml sample was removed from the flask for counting after each mixing, ten such subsamples being taken in all.

Bluegill Distribution

Bluegill were the dominant species in the lake numerically. Our gear

(bottom trawl) appeared to be most effective for sampling this population, which Helm's (1958) studies have indicated are present near the bottom when in open water. Catch per unit effort during the day was relatively constant from April through July at approximately 300 fish per haul (Figure 41). From August through October, greater numbers were taken with a maximum of 860 fish per haul in September. In November the catch per unit effort dropped to 50 fish per haul, the lowest of any month. Night catches remained low (usually less than 100 per haul), except during October, when bluegills were approximately equally abundant in the open water during day and at night.

During the September trawling and shocking series, all fish captured were measured. A sample size of over 1,000 fish for each zone was used to compare the size class distribution in the open water and the littoral zone (Figure 42). Young-of-the-year fish formed a large percentage of the littoral population (88%). However, if only the adult population is considered, the 130mm and over size class formed the greatest percentage of the littoral population (50%), while in the limnetic zone, the two intermediate size classes occur in far greater numbers (32% and 54%). Young-of-the-year were apparently not migrating to the epilimnion of the limnetic zone at this time, as Werner (1969) reported for Crane Lake, Indiana. Surface and midwater trawls also used in the sampling did not catch any bluegill young-of-the-year.

Converting the numbers to biomass by multiplying by the mean weight of the individuals in a length class had the effect of reducing the importance of the 70-99mm fish and increasing the importance of the 135mm and over fish (Figure 43). In the limnetic zone the 100-129mm length class dominated the biomass (56%), while young-of-the-year were of no significance. Young-of-the-year were significant in the littoral zone, however, comprising 16% of the biomass. The 130mm and above fish dominated this region, comprising 63% of the entire population and 73% of the adult population. Both intermediate length classes were of less importance in the littoral than the limnetic zone.

Bluegill Feeding Periodicity

Stomach contents reached a maximum of over 1.2% of the body weight for the 75-95mm length class in the limnetic zone, this occurring at 1900 (Figure 44). Maximum fullness occurred earlier for 105-125mm fish (1600) at a level about one-half as high (0.7%). Large fish from the limnetic zone maintained the same stomach content to body weight ratio as the previous size class through 1000, after which their percentage decreased, leaving the 1000 figure as a maximum (Figure 45). Large bluegill in the littoral zone contained more food than those from the open water, reaching a maximum at 1300 and maintaining a relatively full stomach through 1900. Keast and Welsh (1968) recorded the stomach content maxima for bluegill at 1500. Since they used bluegill ranging from 90-140mm, these data appeared to be fairly consistent with ours. However, their findings that bluegill recommenced feeding at 2030 did not agree with the data on

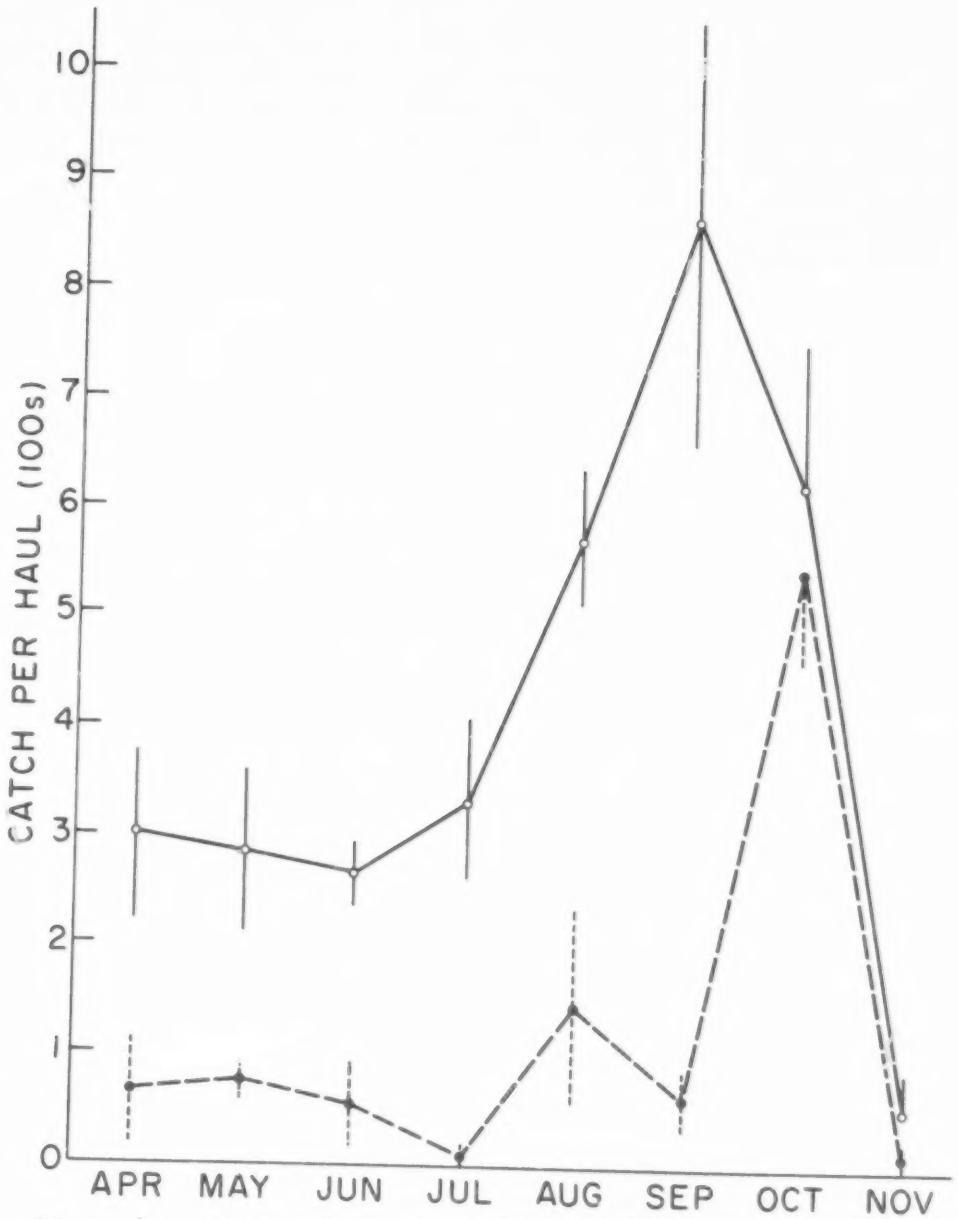

Figure 41. Catch per trawl run day and night for the bluegill (Lepomis macrochirus). Open circles are the mean of the day values with vertical lines for the standard deviation from the mean, and solid circles are the average of the night values with vertical lines for the range. (The sampling consisted of two 24-hour series with day samples at 0800, 1200, and 1600 and with night samples at 0000).

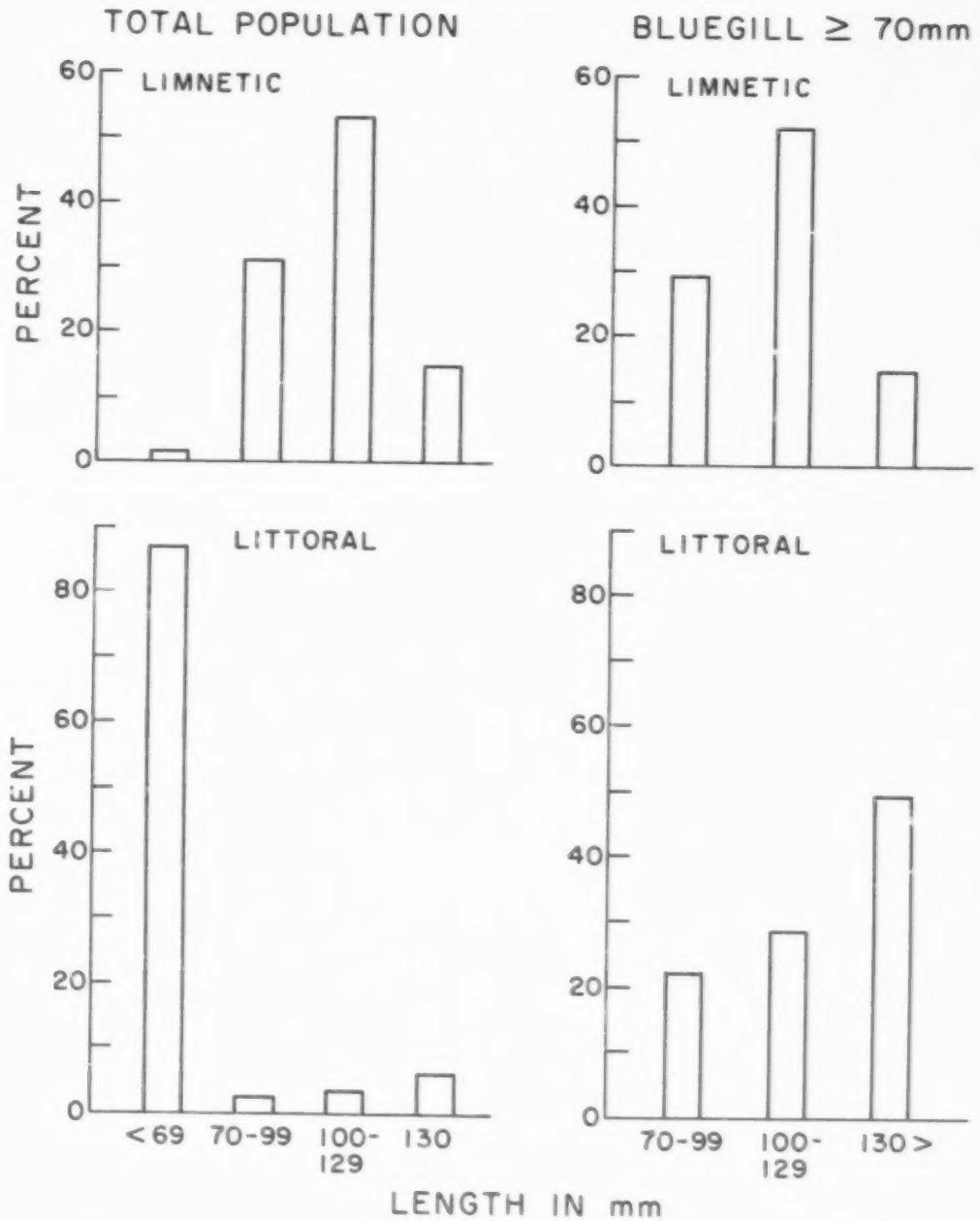

Figure 42. Percent composition by number for size classes of the bluegill population in limnetic and littoral zones on September 17-18, 1970. Percentages were calculated separately for the entire population and for fish 70mm or larger.

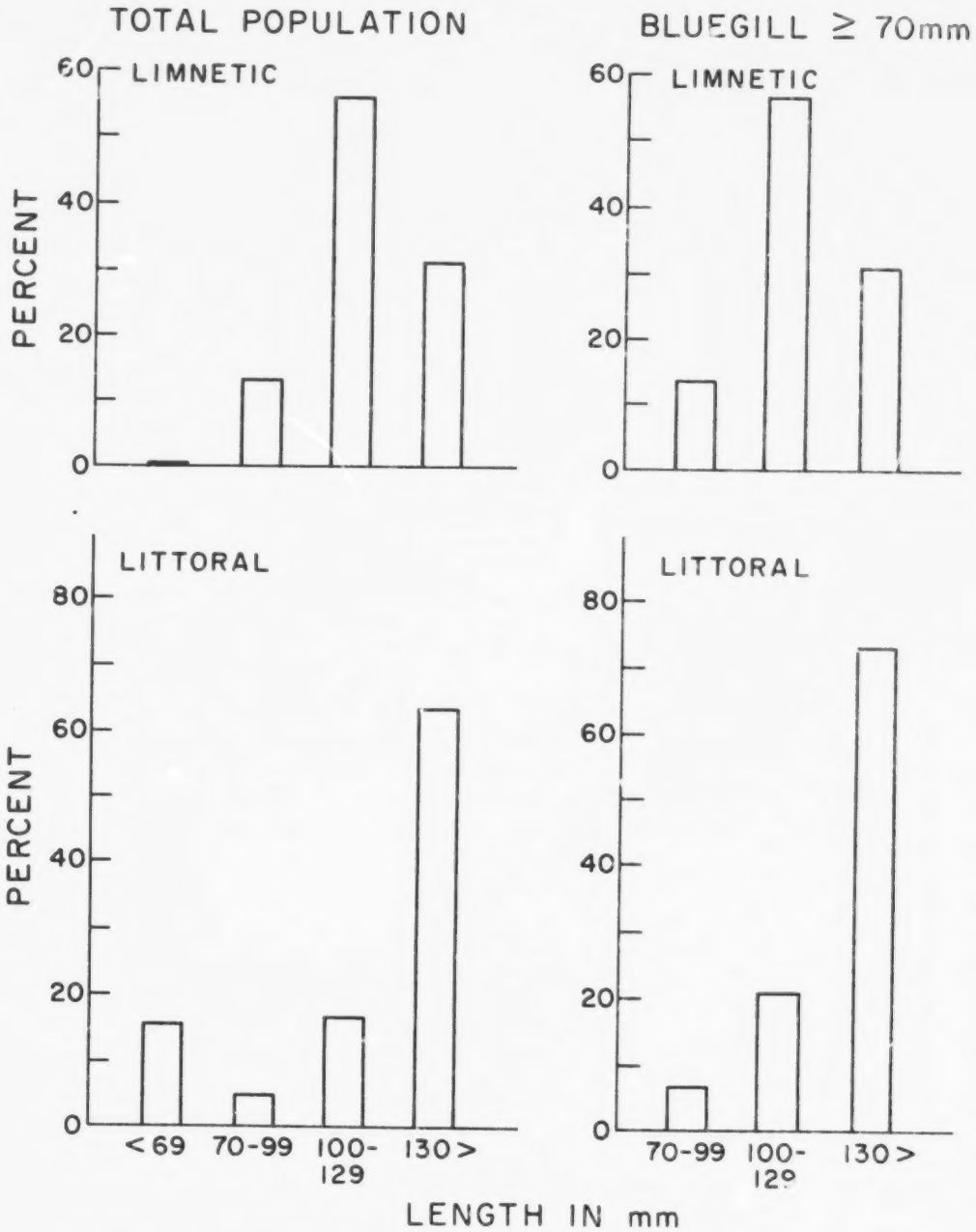

Figure 43. Percent composition by biomass of the bluegill population in limnetic and littoral zones on September 17-18, 1970. Percentages were calculated separately for the entire population and for fish 70 mm or larger.

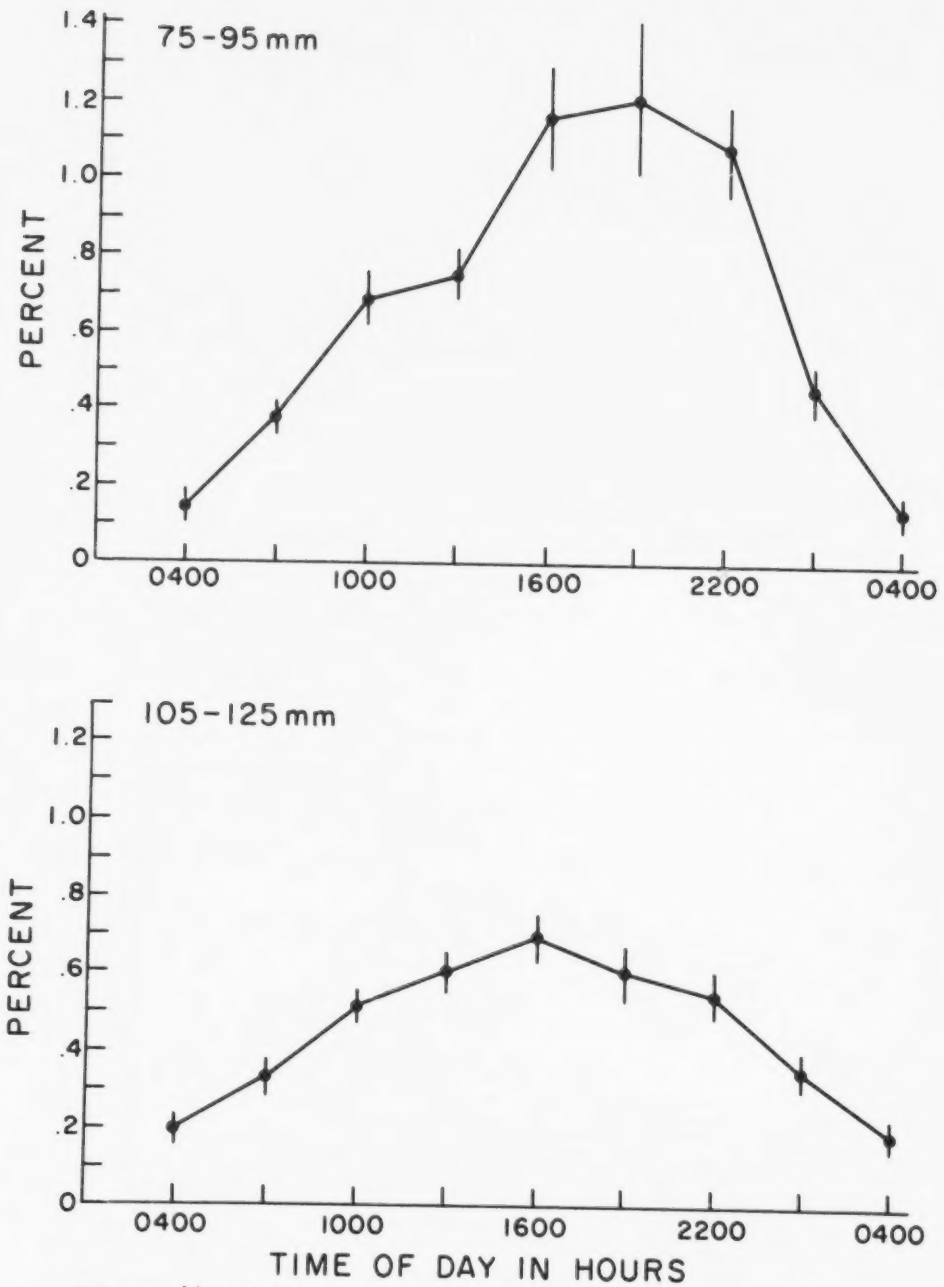

Figure 44. Daily feeding periodicity of two size classes of bluegill in the limnetic zone (September 17-18, 1970). Solid points are percent mean weights (g) of stomach content per gram of fish; vertical lines are standard deviation from the mean.

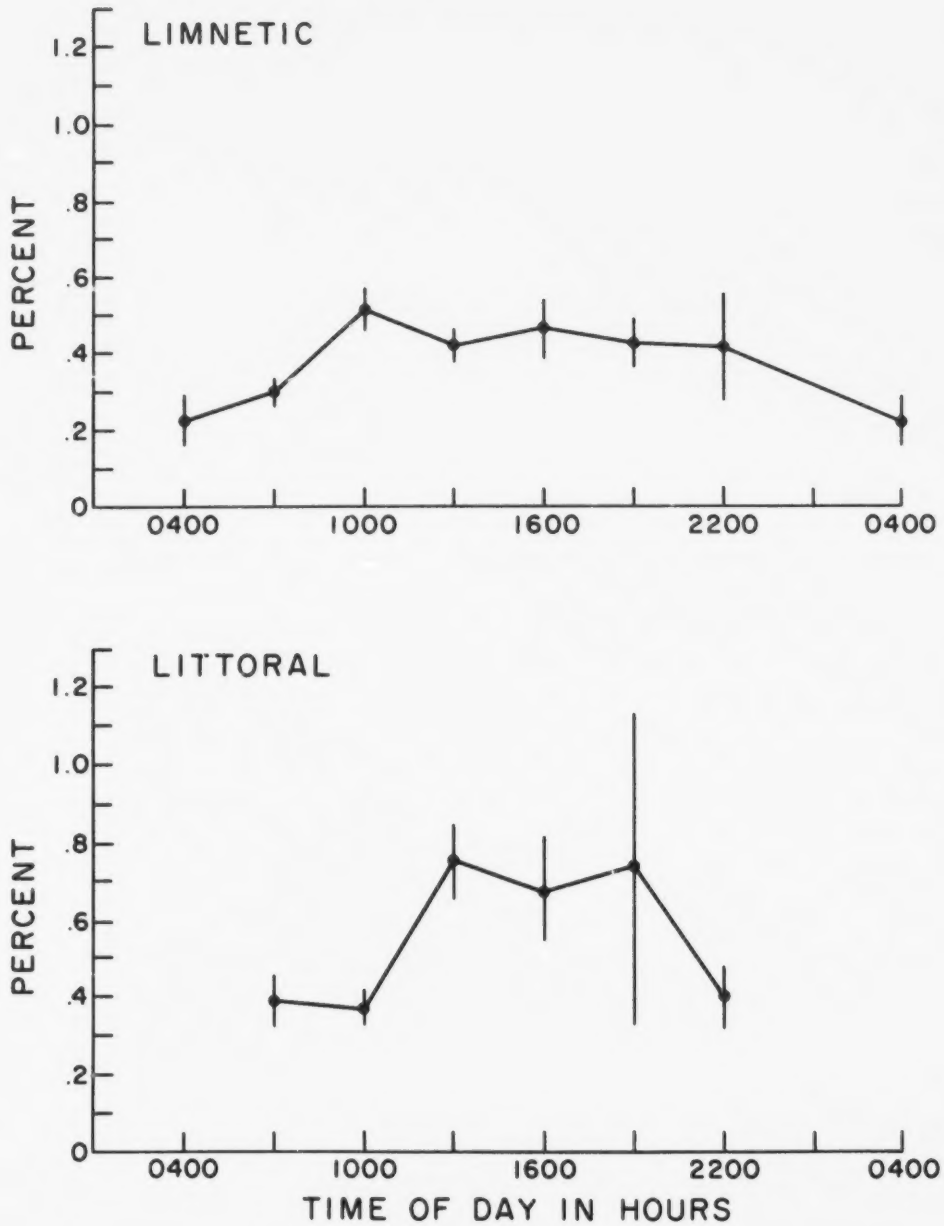

Figure 45. Daily feeding periodicity of 135mm or larger bluegills from the limnetic and littoral zones (September 17-18, 1970). Solid points are percent mean weights (g) of stomach content per gram of fish; vertical lines are standard deviation from the mean.

Figures 44 and 45. This lack of any night feeding in Lake Wingra differed from the results of both Keast and Welch (1968) and Seaburg and Moyle(1964), whose field data indicated fairly constant feeding throughout the 24 hours.

Although a lack of night data precludes calculations, the large bluegill in the littoral zone appeared to have a significantly higher daily ration than those in the limnetic zone. Considering only bluegill caught in open water, the percent of the body weight represented by the stomach contents declines with an increase in size. Smaller fish also reached their maximum values later in the day, indicating a longer feeding period.

If several conditions have been met, the average amount of food consumed between sampling periods can be determined from the average weights of food present in the stomach (Table 4). First, no feeding should have occurred between those sampling periods from which the digestive rate was calculated. Secondly, all the fish sampled must have belonged to the same population. Finally, an assumption must be made concerning the nature of the digestive rate and how it varied with meal size.

We assumed the first two conditions were fulfilled, the second of these being supported by our distribution data. The third assumption created more of a problem. Digestive rates have been under intensive study in recent years, and the literature supports three different points of view. Pandian (1967) stated that the percent body weight per hour digested increased as digestion proceeds, and that the digestive rate was a direct function of time. The results of other investigators, however, demonstrated that the amount of food digested per unit time increased as the meal size increased. Many of these same investigators, though, assumed that once this amount per unit time was determined, it remained constant throughout the period of digestion (Hunt, 1960; Kitchell and Windell, 1968; Windell et al., 1969).

Some recent research indicated that the amount of food digested per unit time also decreased as the food mass remaining in the stomach decreased. Seaburg and Moyle (1964) used this assumption in their calculation of the average daily meal for bluegill. Tyler (1970) fitted both a rectilinear and curvilinear (expcnential) equation to his data on digestion in cod. The negative exponential gave the best fit, meaning that for equal time intervals, equal percentages of the amount present in the stomach would be passed into the intestine. A rectilinear fit would have indicated that a constant quantity is passed per unit time. Thus, in Tyler's study, greater quantities were removed from the stomach in the early hours of digestion than later in the process. Conditioned regressions had also been used to determine digestion rate (McKone, 1971). Again, these indicated that the digestive rate was proportional to the amount of food remaining in the stomach, or that the grams per hour digested were larger for larger stomach volumes.

Most of the literature, therefore, supported a digestion rate which varied with meal size. We assumed a curvilinear function for our data (using

Table 4. Mean weight of food (g) per fish present in the stomach for two length classes of bluegill at different hours during the sampling period (September 17-18, 1970).

				Small Fish				
Time	0700	1000	1300	1600	1900	2200	0100	0400
Weight of Food	.0387	.0693	.0790	.1208	.1331	.1120	.0489	.0159
				Medium Fish				
Time	0700	1000	1300	1600	1900	2200	0100	0400
Weight of Food	.0985	.1509	.1628	.1933	.1739	.1496	.1014	.0522

percent of remaining mass digested per unit time as a constant). If a mechanism did exist (as it seemed to) which could adjust the digestive rate according to the initial meal size, logically this mechanism would also adjust the digestive rate as the size of the initial meal changes. The greatest percent of mass lost between two adjacent sampling periods occurred between 0100 and 0400 for both small and medium-sized bluegill (Table 4). This was 67.5% for the 75-95mm fish and 48.5% for the 105-125mm fish. Although much of the literature stated that the digestive rate was constant for all size classes, smaller individuals were found to have a faster digestive rate by both Seaburg and Moyle (1964) and Pandian (1967).

The amount of food consumed between two sampling periods could be expressed by the equation:

$$A_t = (F/100)(S_t) + (S_{t+1} - S_t)$$

where: A_t = the amount of food eaten between times t and t+1

F = the greatest percent decrease of mass between any two adjacent sampling periods

S_t = the average weight of food per stomach at the sampling period at time t

S_{t+1} = the average weight of food per stomach at the sampling period of time t+1 immediately following sampling period S_t

Solving this equation, a graph of food consumed plotted against time was constructed (Figure 46). The period of least feeding (assumed to be zero feeding) occurred between 0100 and 0400 for both smaller length classes of bluegill. Large bluegill consumption was not determined because of lack of night data. Small (75-95mm) bluegill fed most heavily throughout the afternoon and early evening (1300-1900). Medium (105-125mm) bluegill had feeding maxima extending from 0700 to 1600, with a light depression between 1000 and 1300. Feeding activity seemed to both begin earlier in the day and to decline earlier in the day for this latter length class.

Bluegill Daily Ration

Daily ration was derived from the expression:

$$(1/W) \sum_{t=1}^{n} A_t$$

where: W = the average weight of the fish being studied

n = the number of sampling periods within 24 hours.

Using this equation and Figure 46, the daily ration was calculated to be 3.9% of the body weight for small bluegill, and 1.8% of the body weight for medium bluegill.

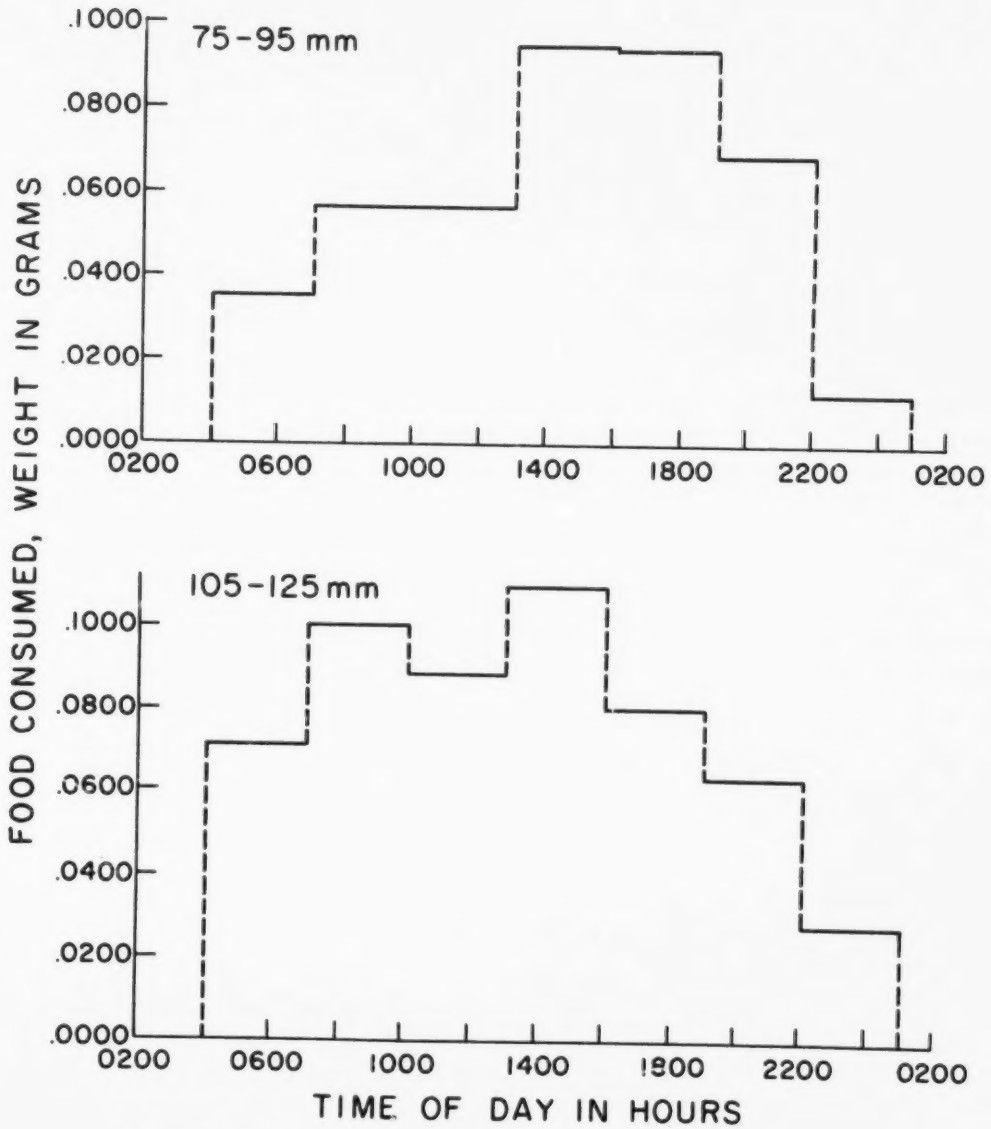

Figure 46. Mean amounts (g) of food consumed between sampling periods (position of dotted lines) for two size classes of bluegill in the limnetic zone (September 17-18, 1970).

Both the digestive rates and the daily rations were slightly higher than most values found in the literature. Gerking (1954) found that a daily ration of 3% was about the maximum for bluegills held in aquaria at room temperature and fed mealworms. Seaburg and Moyle (1964) calculated that the average summer daily ration for bluegill in Grove and Maple Lakes, Minnesota, ranged from 1.4% to 2.2%. Keast and Welsh (1968) reported a daily ration of 2.5% for bluegill in June. Other data from Lake Wingra placed the daily ration in September at 1.38% for small bluegills and 1.18% for medium bluegills (Magnuson and Kitchell, 1971).

Part of the difference between our values and those of Magnuson and Kitchell were probably due to a different definition of the two length classes. Especially in the small length class, fish used by them averaged larger (13.5g) than ours (10.6g). There was also a difference in the average stomach to body weight ratios for that month. Both studies calculated 0.48 for the medium bluegills, but whereas the value of Magnuson and Kitchell for small bluegills was 0.56, ours was 0.73. This difference may have been due to the different sampling periods within the month, or again have reflected the larger fish used by Magnuson and Kitchell.

The rest of the discrepancy originated from a difference in digestive rates. The above study estimated 35% digestion in 3 hours at 19°C. Our field data calculated rate may be too high, especially considering the small (ten fish per period) sample size. (If the first assumption had been violated, i.e., if fish had been feeding between 0100 and 0400, this would have increased not decreased the rate.) However, rates calculated in the lab may be too low. Windell (1967) demonstrated that starvation prior to feeding experiments decreased the rate of digestion. Also, stress produced by handling and confinement might have caused a decrease in digestive efficiency. Therefore, laboratory derived digestive rates might have been lower than those actually occurring in the field. Whether or not our own data were in error, the equations presented should provide a viable method for the determination of daily ration from field data, providing the three assumptions previously mentioned have been met.

Food Organisms Utilized by Bluegill

Qualitative analysis of the stomach contents was carried out for those fish captured by both boom shocker and trawl at 1600 hours September. Bluegill in the littoral zone were selecting macrofood items (predominantly chironomid larvae) while those in the open water were selectively feeding on zooplankton (Figure 47). Ball (1948) also noted that fish feeding on zooplankton did not feed on macrofood items at the same time. In limnetic samples, bluegill of the largest length class contained fewer zooplankters per stomach than small and medium bluegill. Therefore, the large bluegill in this area appeared to be at a disadvantage. Large bluegill did have a greater number of macrofood items per stomach than the smaller length classes, especially in the

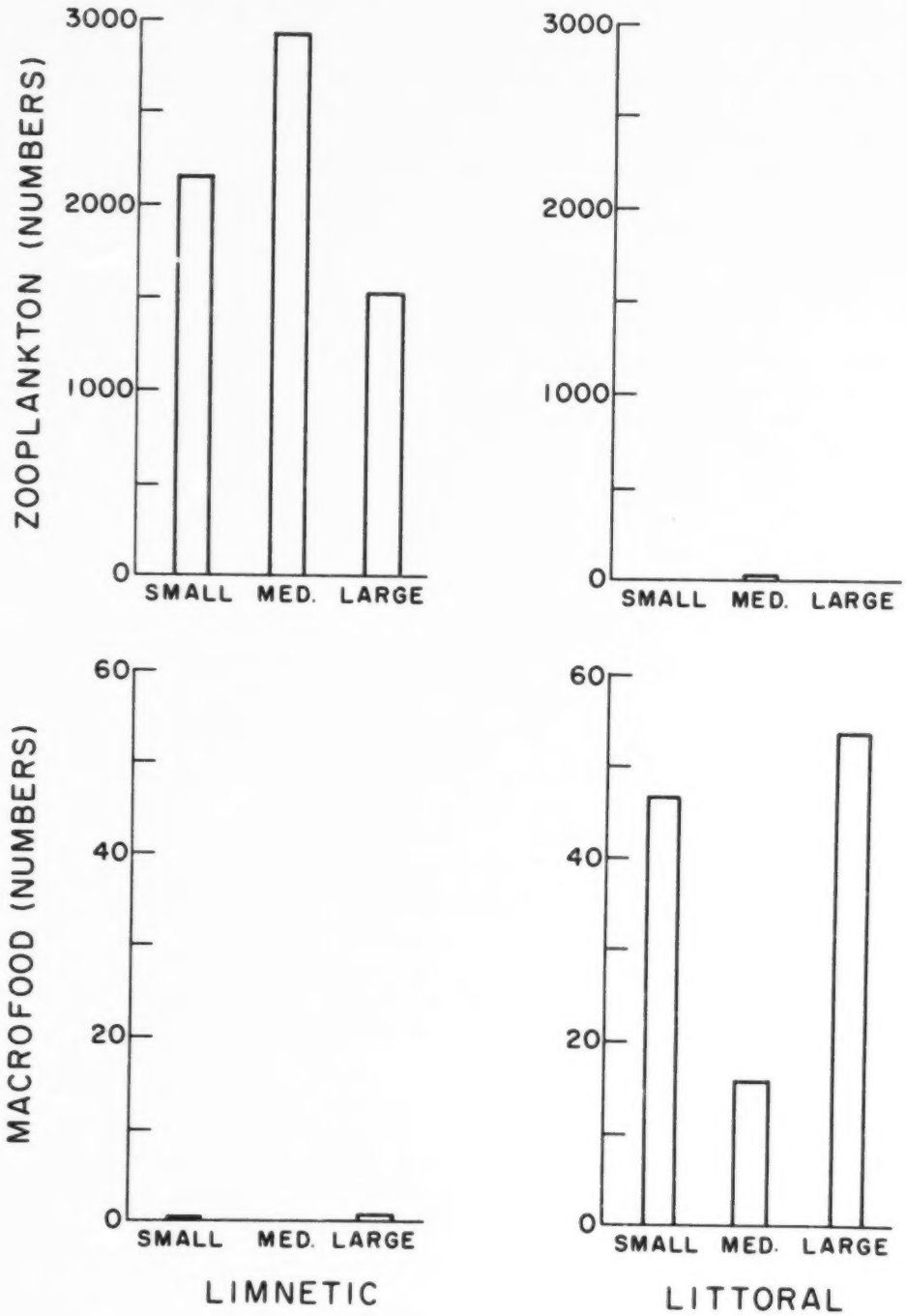

Figure 47. Number of zooplankton and macrofood organisms per stomach for three size classes of bluegill: small (75-95mm), medium (105-125mm), and large (135mm and larger) taken in the limnetic zone September 17-18, 1970).

littoral zone. Unfortunately, we only determined numbers of macrofood items per stomach rather than weights or volumes. Macrofood animals (especially the chironomids) found in large bluegill were bigger than those found in the smaller individuals. Therefore, there would have been an even greater difference between the amount of macrofood per large bluegill compared with the amount per smaller bluegill if weight or volume had been used.

Cladocerans, especially Daphnia retrocurva, were the most abundant zooplankters found in bluegill stomachs (Figure 48). All three size classes of bluegill had approximately the same percentage composition of the various types of organisms. Bosmina sp., however, were only taken to any degree by the smallest size class, while Ceriodaphnia sp. were more common in the two larger size classes. Copepods were scarce, making up less than 1% of the number of zooplanktors in each of the three size classes. Cladocerans have been often reported as an important item in the bluegill diet (Helm, 1958; Gerking, 1962; Seaburg and Moyle, 1964; and Keast and Webb, 1966). Copepods were often also present, although at low levels (Helm, 1958; Gerking, 1962; Keast and Webb, 1966). In Leonard's (1940) study, smaller bluegill fed on zooplankton while the larger fish fed on macrofood items. This was not substantiated by our data from the limnetic zone. Werner (1969 demonstrated that bluegill young-of-the-year in Crane Lake, Indiana, fed almost entirely on planktonic crustaceans, including Daphnia galeata, Ceriodaphnia spp., Bosmina spp., and copepods. Adult bluegill taken during the summer by Ball (1948) utilized Daphnia spp., Ceriodaphnia spp., Diaptomus spp., and Cyclops spp. An important point to notice is the bluegill did not feed on chironomids in open water, even though this organism is available here, as will be shown later by pumpkinseed feeding habits.

Chironomid larvae were the most numerous food organisms for all three size classes of bluegill in the littoral zone (Table 5). Chironomid pupae were also numerous as were Odonata nymphs, other dipteran larvae, and terrestrial insects. Hemipterans were found more often in large fish and mollusks were found more often in 105-125mm fish. Only in the largest size class did fish occur as a food item. Chironomid immatures emerged as a major bluegill food in studies by Helm (1958), Seaburg and Moyle (1964), and Etnier (1971), and as the most important food item in studies by Leonard (1940), Ball (1948), Gerking (1962), and Keast and Webb (1966). Research also demonstrated that bluegill frequently utilize Odonata nymphs (Leonard, 1940; Ball, 1948; Keast and Webb, 1966; and Etnier, 1971), terrestrial insects (Ball, 1948; Keast and Webb, 1966), and Etnier, 1971), mollusks (Ball, 1948; and Keast and Webb, 1966), and fish (Helm, 1958; and Keast and Webb, 1966).

Distribution of Other Panfish

Yellow bass distribution in the limnetic zone was quite different from that of bluegills (Figure 49). From April through July, yellow bass

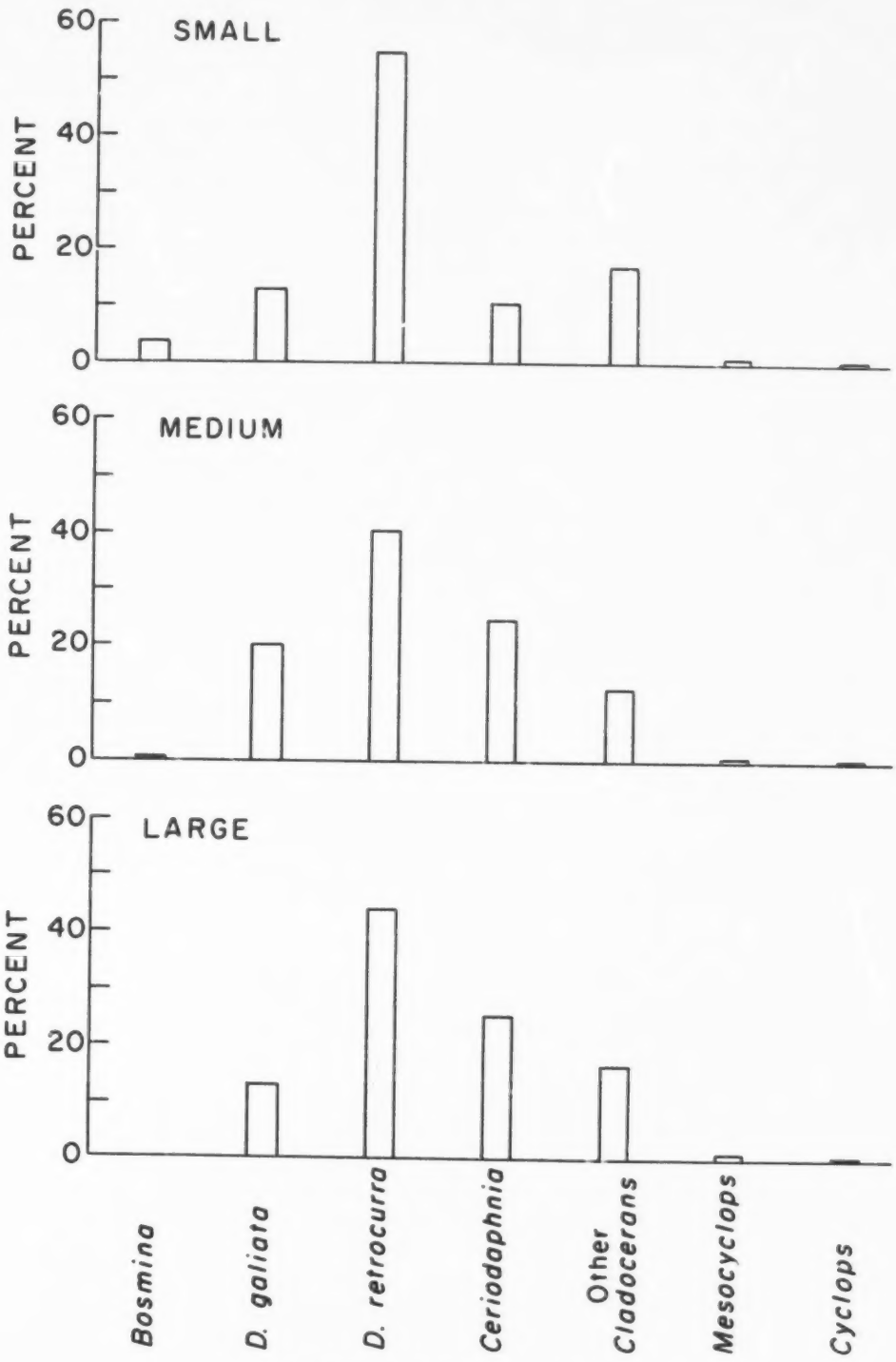

Figure 48. Percent composition by number of species of zooplanktors in stomachs of three size classes of bluegill: small (75-95mm), medium (105-125mm), and large (135mm and larger) taken in the limnetic zone September 17-18, 1970.

Table 5. Mean percent numerical composition of macrofood species per subsample (two fish) for three size classes of bluegill. Each size class represents ten fish taken from the limnetic zone on September 17-18, 1970. Only subsamples containing food were used (two 105-125mm fish did not contain food, i.e., one subsample).

Food Organism	Percent of Total Food 75-95mm fish	Percent of Total Food 105-125mm fish	Percent of Total Food 135mm+ fish
Chironomid Larvae	66.7	48.6	59.8
Chironomid Pupae	5.9	11.8	7.9
Other Dipterans	3.3	5.4	7.1
Odonata	12.6	5.0	11.6
Hemiptera	0.1	1.4	7.2
Terrestrial Insects	8.7	17.4	2.7
Heleidae	0	0.4	0.8
Mollusca	2.1	5.5	1.2
Fish	0	0	0.9
Other	0.5	4.4	0.8
Total Number of Food Organisms	467	139	535

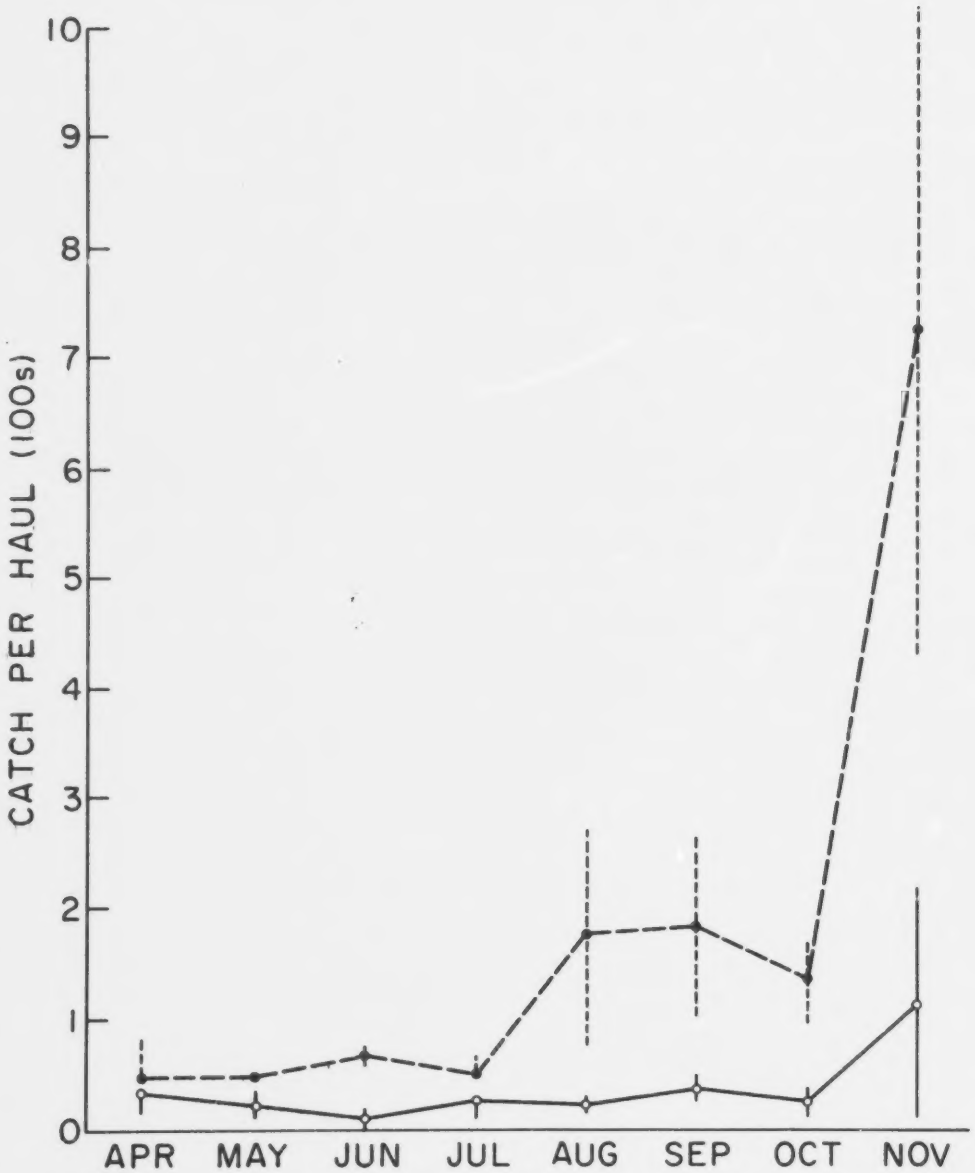

Figure 49. Catch per trawl run day (0800, 1200, and 1600) and catch per trawl run night (0000) of yellow bass (Morone mississippiensis) taken from a 48-hour series. Open circles are the mean of the six day values and vertical lines the standard deviation from this mean. The solid circles are the average of two night values and vertical lines are the range.

were always caught in small numbers. Although night catch per unit effort was always higher, no significant differences between day and night catches occurred during this period. Between August and October, the difference between day and night became substantial. Either the species was now more abundant in the limnetic zone at night or its catchability at night had increased. Finally, in November there was some increase in the day catch and an extremely large increase in the night catch. Helm (1958) also caught more yellow bass at night than during the day. He later electrified his trawl, however, and increased his catch per unit effort of yellow bass by a factor of eight without increasing his catch per unit effort of bluegill. This leads to the conclusion that yellow bass were avoiding the unelectrified gear. The rise in catch per unit effort for yellow bass in November, though, might have indicated an actual increase in abundance. Whether or not this was the case remains unknown.

White crappies reached a maximum abundance in open water in May (Figure 50). After May, the catch per unit effort declined throughout the rest of the sampling period. All samples reflected a greater abundance during the day than at night. Helm (1958) captured white crappie almost exclusively between 0500 and 1900 hours. This species was taken in small numbers compared to bluegill and yellow bass. Multilevel trawling by Helm (1958) showed that white crappie were midway up in the water column rather than being on the bottom. Although we also used a midwater trawl, we didn't obtain any conclusive data. The major portion of the white crappie population could possibly have been above the level at which our gear operated. Therefore, the white crappie population may not have been adequately sampled.

Pumpkinseed distribution (Figure 50) was fairly consistent throughout most of the sample period. Numbers never reached high levels in the open water, since the majority of the population remained in the littoral zone. Although more pumpkinseeds were usually cuaght during the day than during the night, the difference was never great. A maximum abundance seemed to occur in April and a general absence of the species from the open waters occurred in November, coinciding with the disappearance of bluegills from this same area (Figure 41). Most of the pumpkinseed population seemed to remain in the littoral zone throughout the day. Therefore, it is probable that only a small proportion of the population was available to our trawl.

Feeding Periodicity of Yellow Bass and Pumpkinseed

Pumpkinseed had a low percent stomach content to body weight (Figure 51). The pattern appeared to be bimodal, although the spread of the means was not great. Keast and Welsh (1968) also recorded a bimodal feeding periodicity curve for pumpkinseed with one peak at 0800 and another at 1800. Although this agreed well with Figure 51, our data did not show the lower peak which they observed at 0300.

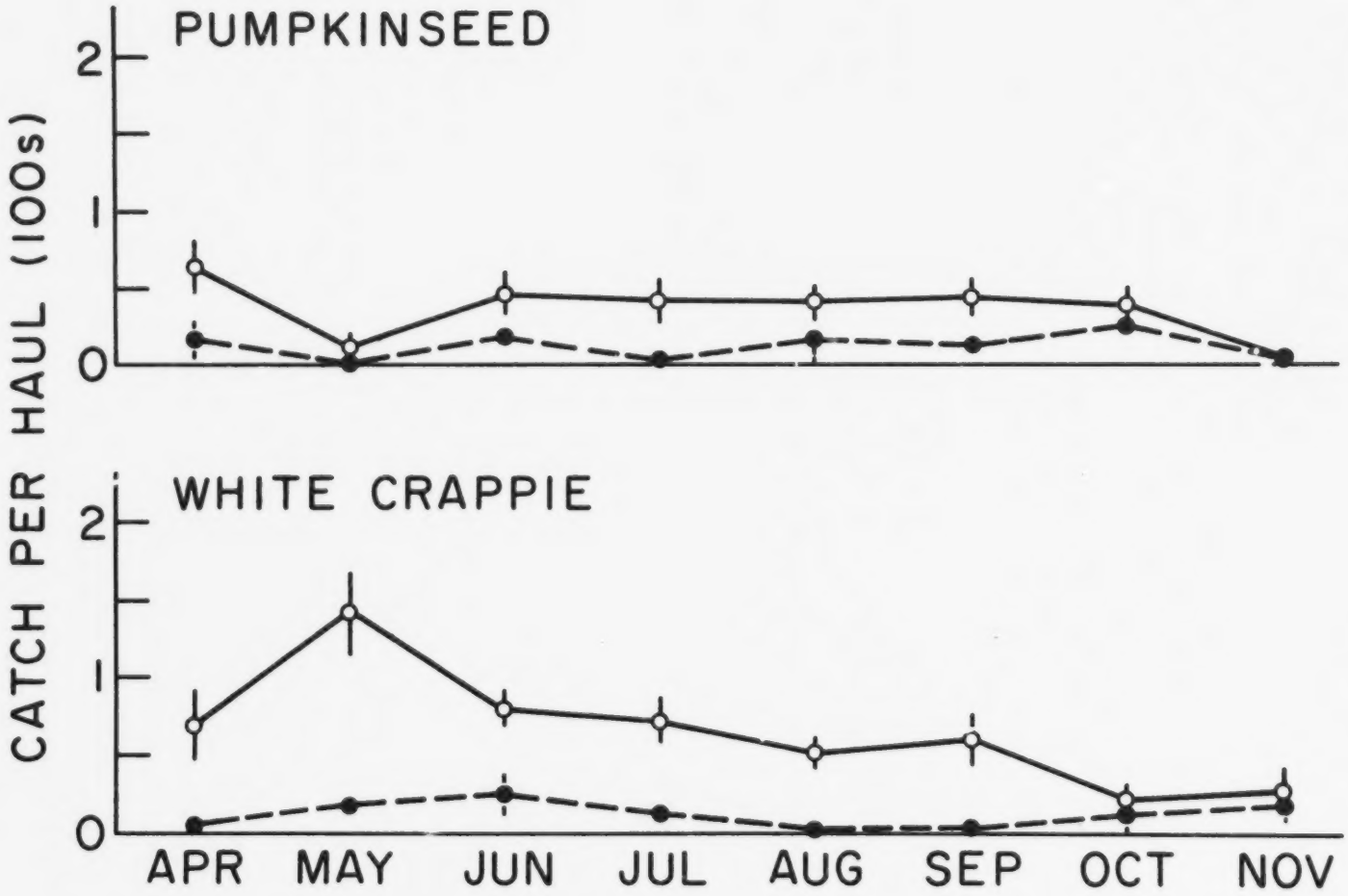

Figure 50. Catch per trawl run day (0800, 1200, 1600) and catch per trawl run night (0000) for two species taken from a 48-hour series. Open circles are the mean of the six day values and vertical lines are the standard deviation from this mean. The solid circles are the average of two night values and the vertical lines are the range.

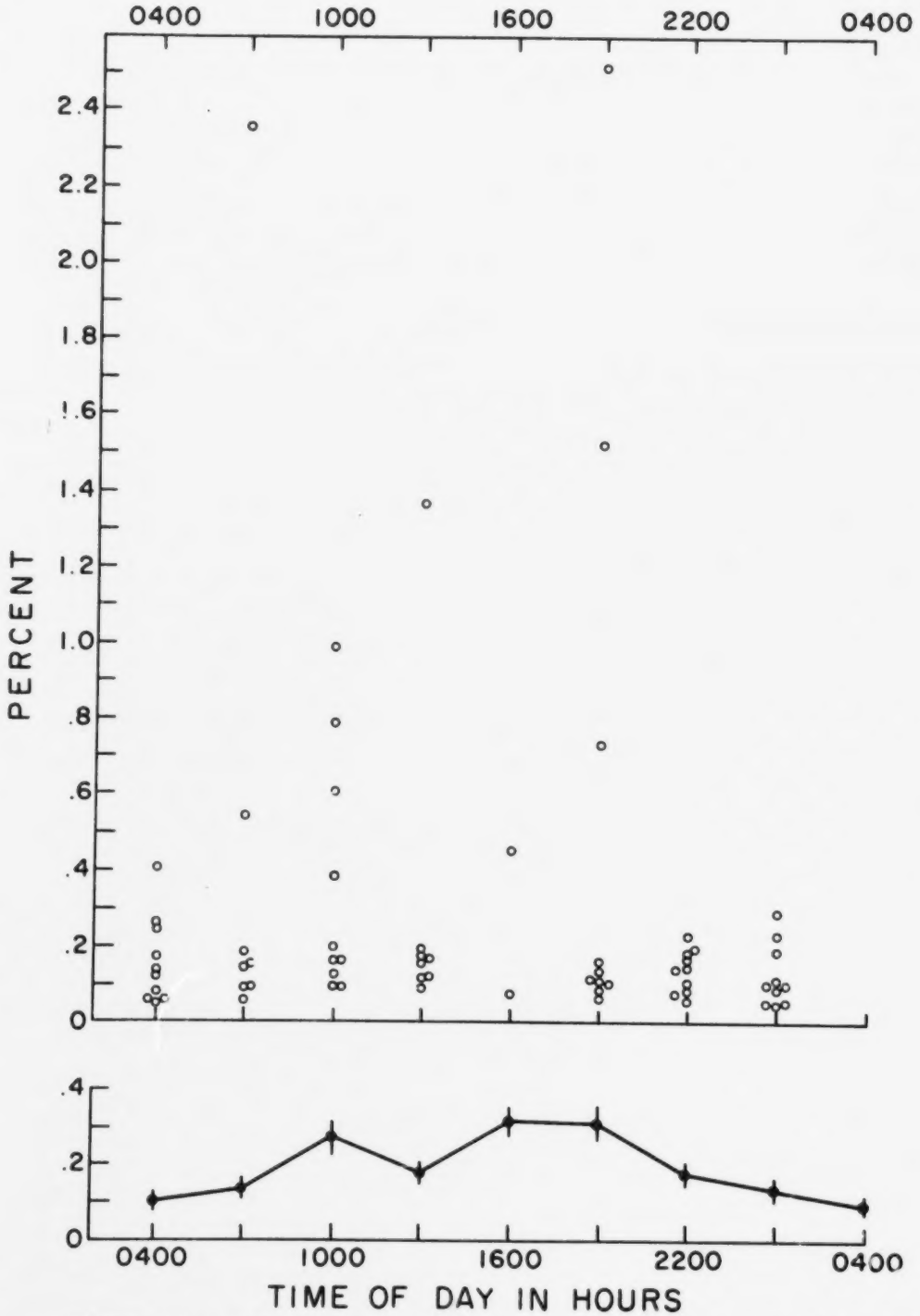

Figure 51. Percent weight (g) of stomach content per weight (g) of fish. Open circles are individual yellow bass; solid points are means for pumpkinseed, and vertical lines are standard deviation from the mean.

Yellow bass percentages were plotted separately for individual fish instead of averaged, because of the great variability inherent in their feeding behavior (Figure 51). The points which were significantly higher than the basal grouping were for fish that had eaten either one or two young-of-the-year Lepomis spp. Over 10% of the sample had fish remains in the stomach. No young-of-the-year were eaten at night, but feeding seemed to continue throughout the day. Previous studies (Helm, 1958) also indicated continuous feeding throughout the day.

Food Organisms Utilized by Other Panfish

White crappies relied heavily on zooplankton for their food supply in open water. Macrofood items occurred only in trace amounts in these stomachs. Over 1/4 of the zooplankters present in white crappie stomachs were Mesocyclops spp. (Table 6). Both Daphnia galeata and Daphnia retrocurva formed significant portions of the diet. Unfortunately, a large number of cladocerans were unidentifiable because of their advanced state of digestion. Zooplankters were also reported by Helm (1958) as being important in the white crappie diet. Marcy (1954) found a predominance of cladocerans in the crappie of Sanctuary Lake, Pennsylvania, while those from the deeper Middle Lake, Pennsylvania, contained a predominance of copepods. First year white crappie studied by Mathur and Robbins (1971) utilized copepods more intensively toward the fall and winter, these organisms comprising 32% of the food by September. None of the white crappie examined in our study contained fish remains. Helm (1958) also failed to find any utilization of fish by the Lake Wingra white crappie population.

Pumpkinseeds fed only on macrofood organisms. These were almost exclusively chironomid larvae, with some chironomid pupae and Heleidae also being utilized (Table 6). Chironomid larvae were frequently reported in the literature as comprising a significant portion of the pumpkinseed diet (Ball, 1958; Seaburg and Moyle, 1964; Keast and Welsh, 1968; and Etnier, 1971). All of these publications also found that snails represented a major food item for pumpkinseed. Since these feeding studies were based on fish captured mainly in the littoral zone, a habitat difference exists which might explain the lack of snails in pumpkinseeds captured for this study.

Yellow bass fed both on chironomid larvae and fish, with fish (young-of-the-year Lepomis spp.) probably being the more important macrofood item as weight or volume (Table 6). Even early researchers reported that yellow bass fed on insects and fish (Burnham, 1910). Helm (1958) found that chironomids and fish were of major importance, but that zooplanktors were equally important. Recent research by Bulkley (1970) indicated that the food preferences of yellow bass changed during the year. Chironomids were utilized heavily from April to July, zooplankton in April and in the winter, and young-of-the-year yellow bass from August to October. Bulkley found that by September 27% of the stomachs contained fish, and these fish comprised 84% of the volume in the stomachs.

Table 6. Mean percent numerical composition of macrofood or zooplankton species per subsample (two fish) for three species. Each species represents ten adult fish taken from the limnetic zone on September 17-18, 1970. Only subsamples containing food were used.

Food Organism	Percent of Total Food Yellow Bass	Percent of Total Food Pumpkinseed	Percent of Total Food White Crappie
Chironomid Larvae	62.5	92.9	
Chironomid Pupae	0	3.4	
Other Dipterans	0	0	
Odonata	0	0	
Hemiptera	0	0	
Terrestrial Insects	0	0	
Heleidae	0	2.9	
Mollusca	0	0	
Fish	37.5	0	
Other	0	0.8	
Total Number of Food Organisms	145	202	
Bosmina sp.			0.2
Daphnia galeata			17.4
Daphnia retrocurva			21.2
Ceriodaphnia sp.			6.3
Other Cladocerans			25.4
Mesocyclops sp.			27.4
Diaptomus sp.			0.1
Cyclops sp.			1.9
Total Number of Food Organisms			24,080

Perhaps the greater use of zooplankton shown by Helm was due to the fact that much of his sample was caught earlier in the year.

Migrations and Seasonal Distribution Patterns

Reports of diel migrations or movements of fish within lakes were common in the literature. Some of these migrations were definitely associated with a migrating or changing food source (McNaught and Hasler, 1961), and some appeared to be correlated with temperature changes (Crossman, 1959a and Crossman, 1959b). Others, including bluegill migrations, appeared to be a response to changing light intensities (Hasler and Bardach, 1949; John, 1959; Davis, 1964; and Werner, 1969).

Since several of the species in Lake Wingra apparently varied greatly in abundance from month to month, changing effectiveness of the gear must be considered. Catch per unit effort is based on a set of assumptions regarding the catchability of the populations being studied. If any of these assumptions are incorrect, then the conclusions drawn from the data will be invalid (Robson and Regier, 1971). That the gear used will be equally effective in capturing all of the species being studied is one such assumption of major importance. Selectivity of the gear can result from extrinsic factors (type of gear, methods of handling the gear, etc.) or intrinsic factors (behavior differences among or within species, differences due to sex or size, time of day sampled, season, etc.) or an interaction between these factors (Lagler, 1971).

Extrinsic factors were reduced by the use of catch per unit effort as only a relative measure of abundance. The limnetic and littoral zones were sampled separately, and samples were taken every three or four hours in a twenty-four hour series, eliminating time of day as a factor. Some error in the trawling statistics was probably introduced, though, by extrapolation from the population at the bottom of the lake to that of the entire limnetic zone. White crappie, for instance, may have been concentrated above the area effectively sampled by the trawl. Therefore, the relative abundance estimated for white crappie may have been low. Yellow bass could probably escape the trawl during the day thereby also appearing to be fewer in number than was naturally the case.

For all the species other than yellow bass, a consistently greater catch per unit effort occurred during the day than at night (when the fish should have had more trouble avoiding the gear). This lent credence to the effectiveness of the gear on those fish available to it. Another concern was whether a consistent amount of effort was used each month. This was supported by the greatest catch per unit effort of the different species occurring in different months. The greatest catch per unit effort of yellow bass occurred in November, when the smallest catches of bluegill occurred (Figures 41 and 49). Pumpkinseed and white crappie (Figure 50) had maxima in April and May, respectively.

Almost all the fish taken in the monthly trawl series were released. The removal of the more vulnerable fish from the population, therefore, should not have been a problem. During any one month, the same area in the limnetic zone was, however, frequently sampled. A decrease

in catch might, therefore, be expected in later runs due to the earlier disturbances. The twenty-four hour series, though, was spaced out over a week, and this bias would also have been consistent for each month.

Boom shocking was selective for larger fish, smaller fish having less voltage drop from head to tail. The crew members dipnetting fish may also have been unconsciously selecting the larger specimens. However, the great numbers of young-of-the-year bluegill taken by this method indicated that these biases were probably not very great. Certain species also seemed better able to break free from the electric field due to a faster swimming rate.

Intrinsic factors which might have influenced the data included varying catchability with changing seasons of environmental conditions (Ricker, 1958). The sudden increase in the catch per unit effort of yellow bass in November (Figure 49) might have been caused by colder water temperatures. This temperature decrease might have slowed the fish to the point that they were then vulnerable to a gear (bottom trawl) which they had been able to avoid previously. If so, however, this only emphasized the decrease in the limentic bluegill population at this time (Figure 41). A seasonal factor that would make a previously unobtainable species easily catchable seems highly unlikely.

A change in environmental conditions could also affect a species' catchability. Helm (1958) stated that white crappie may rise in the water column on cloudy days. If this is true, a month in which the sampling was done in cloudy weather might show a false drop in the limnetic crappie population. The fish normally caught may simply have moved above the level sampled by the gear. No serious decreases in the population size were actually shown by the data however (Figure 50). Even considering all of these possible biases, some actual changes in the distribution patterns of fishes in the lake were pointed out by the data. Among these were the differences in day as opposed to night catch per unit effort and the different directions of change in the bluegill and yellow bass population distributions in November.

Therefore, if our data accurately represent the situation in Lake Wingra, a significant portion of the bluegill population was migrating into the limnetic zone during the day and returning to the littoral zone at night (Figure 41). This movement seemed to intensify in late summer and then disappear in November. Combining this information with the inshore data (Figure 42) led to the conclusion that the participants in the migration were largely from the two intermediate size classes. A greater proportion of the young-of-the-year and large fish seemed to remain in the littoral zone. This distribution for the young-of-the-year could be expected, since the dense vegetation beds offered a great deal of protection.

Yellow bass also engaged in diurnal onshore-offshore movements in certain situations (Carlander and Cleery, 1968). Helm (1958) noted an evening

onshore movement in Lake Wingra. The data from our study were not conclusive, since it appeared that most yellow bass were able to escape the gear in the daytime (Figure 49).

Food Utilization among Different Size Classes of Bluegill

Bluegills of all three size classes utilize the same types of food when they are present in the same habitat (Figures 47 and 48, Table 5). All bluegills in the limnetic zone fed on zooplankton, which the small and medium sized fish obtained in much greater numbers. Conversely, all adult bluegills in the littoral zone fed on macrofood organisms, largely chironomid larvae. Here the largest bluegill appeared to be the most successful feeders.

This was also demonstrated by the stomach to body weight ratios, higher for those bluegill greater than 135mm caught in the littoral zone than for the same size class caught in the limnetic zone. The ratio for this group in open water was far lower than the ratios for the two smaller size classes. Therefore, there appeared to be an advantage for bluegills of large size to remain in the shallow water and not to participate in the migration to the limnetic zone during the day. A large percentage of this upper size class did appear to remain inshore (Figure 42).

Food Utilization among Different Species

In the limnetic zone, adult white crappie fed almost exclusively on zooplankton. Only bluegill, of the species studied, also utilized this food source in open water. However, the white crappie appeared to select a much greater proportion of copepods than did the bluegill (Figure 48, Table 6), thereby minimizing the overlap of food organisms.

Pumpkinseeds utilized chironomid larvae as their main food item in the limnetic zone. Yellow bass fed on chironomids as well, but also preyed on young-of-the-year Lepomis spp. (Table 6). Since the pumpkinseed population was sparse in the limnetic zone, little if any competition could be possible even with the similarity in diet. Except for yellow bass, none of the fish studied, including the white crappie were piscivorous in the limnetic zone.

The Effect of Interactions Between Lake Wingra's Fish Species on the Ecosystem's Energy Flow

Some of the interactions of the Lake Wingra fishes in mid-September could now be summarized. Most of the bluegills between 70mm and 135mm took part in a diel migration to the limnetic zone each morning. While in the open water, these fish concentrated near the bottom where they fed on zooplankton. Here they were associated with yellow bass which may also take part in at least a partial migration). The yellow bass preyed on both young-of-the-year Lepomis spp. and chironomid larvae. Pumpkinseed were also

present in this area in small numbers, feeding on chironomids. Dispersed slightly above this level were the white crappie. These fish were feeding on zooplankton, but due either to selection or a vertical distribution of zooplankton species, they preyed far more heavily on Mesocyclops spp. than did the bluegill.

Most young-of-the-year and large bluegill remained in the littoral zone. Here the large bluegill cropped chironomids and other macrofood organisms. Pumpkinseeds in the littoral zone probably fed on chironomids and snails (Ball, 1948; Seaburg and Moyle, 1964; Keast and Welsh, 1968; and Etnier, 1971). According to Helm (1958), yellow bass also utilized the chironomids in this area as part of a diet which again included small fish.

White crappie were largely replaced by black crappie in the littoral zone. Fyke net catches of May, 1969, contained more black crappie than any other species (28% of the total catch). White crappie composed only 7% of these littoral samples. In open water, black crappie were only caught infrequently and in low numbers. A spatial segregation of these two species appeared to be present in Lake Wingra. Food habits of both these fish in the littoral area were not well known.

At dusk most bluegill returned to the littoral zone, but did very little feeding during the night. Digestion did occur, however, and nutrients from the limnetic zone were deposited by the bluegills in the littoral area as feces and urine. Pumpkinseeds also fed almost entirely during the day (Figure 51; Spencer, 1929). Yellow bass (some of which may have also traveled to the littoral zone) continued to feed through the night, although fish were then no longer part of the diet.

These relationships were obviously dependent upon seasonal changes. The catches per unit effort indicated that the situation in early summer was probably quite different from that in September. Changes of migration patterns with the time of year have been recorded for perch (Hasler and Bardach, 1949) and for redside shinner (Crossman, 1959a). Changes of food items from month to month have been reported for bluegill (Gerking, 1962; Seaburg and Moyle, 1964), yellow bass (Bulkley, 1970), and white crappie (Mathur and Robbins, 1971). Preliminary data from Lake Wingra also indicated monthly changes in the food of all major panfish species (Magnuson and Kitchell, 1971).

Conclusion

This study, therefore, points out the great complexity of interaction which exists between units in the ecosystem. Data extrapolation and ecosystem modeling should be done remembering the limitations indicated by our study. Littoral zone and open water habitats should be studied separately to get a good average of the feeding habits of those fish species which occupy both areas. These feeding habits, as well as the population structure, will also change from month to month, thereby requiring sampling over the

entire year to obtain an accurate yearly average. Different size classes of a species must also be studied separately to document the changes in food preference and habitat which often occur with growth.

The implications of these data are that models of whole lake ecosystems must account for the mobility of predators in estimating their impact on prey populations characterized by differing spatial and temporal susceptibilities to predation.

SECTION VIII

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SECTION IX

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